

THE FLORAL MORPHOLOGY AND VASCULAR ANATOMY OF THE HAMAMELIDACEAE: SUBFAMILY LIQUIDAMBAROIDEAE¹

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ABSTRACT

Inflorescence and floral morphology and floral vascular anatomy of the subfamily Liquidambaroideae (*Liquidambar* L., *Altingia* Nor.) are described. The inflorescence appears to be a greatly condensed compound raceme with proximal pistillate heads and distal staminate heads. Functionally pistillate flowers contain sterile or even fertile stamens. Functionally staminate flowers may show evidence of partially developed gynoecia. There is no morphological or anatomical evidence of sepals or petals. In functionally pistillate flowers a cycle of sterile phyllomes of uncertain nature (staminodia?, disc lobes?) is inserted on the hypanthium between the stamens and carpels of the partly inferior ovary. In pistillate flowers the stamens derive a single trace and the phyllomes a ramifying system of bundles from hypanthial trunk bundles. Each carpel contains a dorsal and two ventral bundles. Numerous ovules on each carpel margin receive traces from the ventral bundles. The gynoecium is interpreted as the most primitive within the Hamamelidaceae, and subfamilial status of Liquidambaroideae, rather than segregation as the family Altingiaceae, is supported.

There has been an increase in interest and discussion in recent years concerning the nature and origins of the "Amentiferae"—a group now accepted by a majority of modern systematists as being made up of highly advanced and specialized taxa—and how they relate to more primitive groups of angiosperms. Central to this problem are the nature and position of the family Hamamelidaceae, which occupies an intermediate position in the various theories and phylogenetic schemes that have been put forth. However, any considerations of the phylogenetic position of the Hamamelidaceae, and of the trends of specialization both within and without the family, must begin with a reasonably clear understanding of which members of the family are primitive, or most nearly so, and which are advanced. At present, opinion is divided on this point and on circumscription of the family. This is due to the remarkable morphological diversity evident

among the 28–30 genera that are now known to comprise the five distinct subfamilies traditionally included in the family. Such diversity is particularly evident among the seven genera that make up the four small subfamilies Liquidambaroideae (Altingioideae of Cronquist, 1981), Rhodoleioideae, Exbucklandioideae (formerly Bucklandioideae or Symingtonioideae of some authors, including Chunioideae of Takhtajan, 1980, and Mytilarioideae of H. T. Chang, 1973), and Disanthoideae.

Each of these subfamilies, and the Liquidambaroideae in particular, is characterized by interesting combinations of primitive and advanced morphological and anatomical features that have led to varying interpretations of their relationships and relative phylogenetic positions. Thus, *Altingia* and *Liquidambar*, comprising the subfamily Liquidambaroideae, have been removed by some workers (e.g., Blume, 1828;

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Hayne, 1830; Lindley, 1836; Wilson, 1905; C. T. Chang, 1959, 1964; Melikian, 1971, 1973a, 1973b; P. R. M. Rao, 1974; T. A. Rao & Bhupal, 1974; Skvortsova, 1960) from the Hamamelidaceae as a segregate family Altingiaceae. Others have considered *Liquidambar* and *Altingia* to be relatively primitive taxa within the Hamamelidaceae (e.g., Makarova, 1957; Schmitt, 1965; Meeuse, 1975), whereas such recent authors as Schulze-Menz (1964), Cronquist (1968), and Takhtajan (1969) considered these genera as relatively advanced members of the Hamamelidaceae. Similarly, Willis (1966) and Wolfe (1973) segregated *Rhodoleia* as a family Rhodoleiaceae, principally on the basis of leaf architecture. Cronquist (1968), while maintaining the Hamamelidaceae in the broad sense, stated that "the monotypic genus *Disanthus* has at least as much claim to family status as the Altingiaceae." The most extreme position is that of Nakai (1943), who went so far as to elevate all four subfamilies to family status, thus restricting the Hamamelidaceae to the genera of subfamily Hamamelidoideae.

With regard to what constitutes the most primitive floral type within the family, Takhtajan (1969) stated that *Disanthus cercidifolius* Maxim., the sole member of the subfamily Disanthoideae, "is the most primitive in floral structure." Cronquist (1968) considered *Disanthus* as "clearly the most primitive" genus in the family, or (Cronquist, 1981) that it "may be the most archaic surviving genus." This view of the primitive nature of *Disanthus* is concurred in by Wolfe (1973) on the basis of leaf architecture (apparently assuming the exclusion of *Rhodoleia* from the Hamamelidaceae), and by Goldblatt and Endress (1977) on evidence from chromosome counts.

Unfortunately, there is still relatively little basic information available in the literature from comparative morphological and anatomical studies of a comprehensive nature on these relatively primitive members of the family. More data are needed before suppositions concerning primitive or advanced conditions, and the morphological limits of the Hamamelidaceae, can be made with any assurance and employed in considerations of extrafamilial relationships.

This paper is intended to present an account of the floral morphology and vascular anatomy of the two genera comprising the subfamily Liquidambaroideae (*Liquidambar*, *Altingia*) based on original anatomical work and morphological

observations, as part of an effort to provide comparable data for all genera of the family. Some observations concerning the little known segregate genus *Semiliquidambar* are also presented.

MATERIALS AND METHODS

Inflorescences of *Liquidambar* and *Altingia* in various stages of development have been collected from both wild and cultivated trees in southeast Asia, and North America either by me, or for me by others. In addition, inflorescences from herbarium specimens in the Arnold Arboretum (A) have also been examined, including those attributable to *Semiliquidambar*. The specimens examined, collection data, and location of voucher specimens are listed in Table 1.

The methods of preservation, preparation and staining of sections, and clearing of floral parts are standard and have been described previously (Bogle, 1970).

I have examined both sectioned and cleared specimens of staminate and pistillate flowers and inflorescences of *Liquidambar* and *Altingia* in anthesis and post anthesis stages.

Drawings were made with the aid of the drawing attachments designed for the Wild M-20 and M-5 microscopes.

I am grateful to the directors and curators of the following arboreta and herbaria for permitting me to use their living and herbarium collections, and for supplying material for the study: Arnold Arboretum of Harvard University; Gray Herbarium of Harvard University; Morris Arboretum of the University of Pennsylvania; Scott Foundation of Swarthmore College; University of Washington Arboretum, Seattle; and the Royal Botanic Gardens, Kew, Great Britain.

RESULTS

In the following paragraphs, the descriptions of the vasculature of the functionally pistillate flowers (hereafter referred to simply as pistillate flowers) are based primarily on serial sections, whereas those of the functionally staminate flowers (hereafter referred to simply as staminate flowers) are based primarily on cleared material. Emphasis is given here to the functionally pistillate flowers because these are, in fact, morphologically and sometimes functionally perfect and more useful for comparison with flowers of the other subfamilies. The staminate flowers, in contrast, appear to represent the culmination of a line of reduction from the perfect condition within the subfamily.

TABLE 1. Collections on which anatomical and morphological observations presented here are directly based (A = Arnold Arboretum, ALB = author's collection).

Taxon	Collector	Locality	Deposited
<i>Altingia chinensis</i> (Champ.) Oliver	<i>Bogle 583</i>	Hong Kong Botanical Garden	ALB
	<i>Bogle 588</i>	Hong Kong, forest above Peel Rise, off Aberdeen Road	ALB
	<i>Bogle 591</i>	Hong Kong, forest above Peel Rise, off Aberdeen Road	ALB
	<i>Hu 6700</i>	Hong Kong	ALB
<i>Altingia chingii</i> Metc.	<i>Pételot 5944</i>	Tonkin, Chapa, 1,500 m	A
	<i>Lau 4356</i> (paratype)	China, Kiangsi	A
	<i>Tso 20760</i>	China, N. Kwangtung, Lok Chong, Yao Shan	A
<i>Altingia excelsa</i> Nor.	<i>Bogle 313</i>	Malaya, Pahang, Cameron Highlands, Mentigi Forest Reserve	ALB
	<i>Abbe 10298</i>	Malaya, Pahang, Cameron Highlands, Mentigi Forest Reserve	ALB
<i>Liquidambar formosana</i> Hance	<i>Bogle 610</i>	Taiwan, Yin-Ping, between Chitow and Chushan	ALB
<i>Liquidambar orientalis</i> Mill.	<i>Bogle 973</i>	USA, Minnesota, Minneapolis, cultivated specimen in Univ. of Minnesota greenhouse	ALB
<i>Liquidambar styraciflua</i> L.	<i>Bogle 790</i>	USA, Pennsylvania, Montgomery Co., Willow Grove, Red Barn Road	ALB
	<i>Bogle 823</i>	Mexico, Hidalgo, vic. El Barrio Road, km 322, S of Tamazunchale	ALB

SUBFAMILY LIQUIDAMBAROIDEAE

Two (or three) genera of large trees make up this distinctive subfamily. The most well known of these, and the most widespread in both living and fossil form, is *Liquidambar* L., which is characterized by its palmately-lobed and -veined, deciduous leaves. *Liquidambar* is disjunctly distributed in eastern Asia, Asia Minor, and in North and Central America.

Less well known is *Altingia* Nor., which differs from *Liquidambar* in its simple, elliptic to oblong, pinnately-veined, evergreen leaves. *Altingia* is widely distributed in southeast Asia.

The segregate genus *Semiliquidambar* H. T. Chang (including *Altingia chingii* Metc.) was established (H. T. Chang, 1962, 1973) to include specimens whose leaf morphology is intermediate between that of *Altingia* and *Liquidambar*. These species are described as having leaf blades that vary from undivided to 2- or 3-lobed, tripinnate venation, and with pistillate flowers lacking staminodia, among other morphological features. I have seen specimens of *Altingia chingii* in which the leaves appear to bridge the gap in leaf shape between *Altingia* and *Liquidambar*

(*Tso 20760*, paratype, A; *Lau 4356*, A; see also Metcalf, 1931, pl. 58; and description of *A. chingii* var. *parvifolia* in Chun, 1934). These genera are in need of monographic revision to better define the number of species and clarify the validity of *Semiliquidambar*. I have not had access to floral material of *Semiliquidambar* suitable for detailed morphological and anatomical work.

Liquidambar and *Altingia* share several morphological and anatomical characteristics, including: gum ducts associated with the vascular bundles of the stems, leaves, and floral organs; formation of terminal buds enclosed within numerous bud scales; spirally arranged stipulate leaves; stipules mounted on the petiole rather than on the stem; extremely condensed, complex, bisexual inflorescences containing numerous many-flowered heads; flowers naked, perfect, or imperfect, and functionally pistillate or staminate; a cycle of sterile organs surrounding the ovary in pistillate flowers; pollen grains polyporate (porate); ovules numerous, inserted on both carpel margins, but only the lowermost one or two on each margin fertile; and seeds winged. This combination of characteristics sets the

subfamily quite apart from the rest of the family, but specific characteristics (e.g., gum ducts, complex inflorescences, sterile floral organs, polyporate pollen grains) do occur in certain genera of the other subfamilies, so are not unique to the *Liquidambaroideae*. For descriptive purposes I shall use the generalized term *phyllome* (cf. Esau, 1965: 424) in reference to the cycle of sterile organs as they appear in *Liquidambar* and *Altingia*, because they are not clearly either staminodial or carpellary in nature.

1. *Liquidambar* L., Sp. Pl. 2: 999. 1753. Figures 1A, 2, 3, 4A-F, 6A-D, I, J.

The genus *Liquidambar* consists of two to five species of large deciduous trees distributed in the Northern Hemisphere. *Liquidambar formosana* Hance is widespread in eastern Asia (Tardieu-Blot, 1965; Li, 1977; H. T. Chang, 1962, 1973). *Liquidambar acalycina* occurs in at least nine provinces of China (H. T. Chang, 1973, 1979). *Liquidambar orientalis* Mill. is known from Turkey and some islands of the Aegean Sea such as Rhodes (Rechinger, 1943) and Cyprus (Holmboe, 1914; Meikle, 1977, as *L. styraciflua*). *Liquidambar styraciflua* L. is widely distributed in eastern and southeastern North America and southward at high elevations on the mountains of Mexico and Central America to Honduras (Little, 1971, map 135-E, 135-N). The Mexican and Central American plants are recognized by some authors as a distinct species, *L. macrophyllum* Oerst. (Sosa, 1978). The three principal species (*L. formosana*, *L. orientalis*, *L. styraciflua*) are also widely cultivated as ornamental trees and form the basis for my observations.

The stipulate leaves of all three species are palmately-lobed and -veined, but differ in the degree of lobation and pubescence. The leaves of *Liquidambar formosana* are usually 3-lobed, those of *L. styraciflua* are usually 5(-7)-lobed (see Duncan, 1959, for a detailed analysis of leaf form in *L. styraciflua*), whereas those of *L. orientalis* are also 5(-7)-lobed, but with the lobes further subdivided. Leaf form in the last two species is intergrading, however, and some authors consider them conspecific (Rechinger, 1943; Meikle, 1977).

Harms (1930, see also H. T. Chang, 1979) recognized two sections within the genus. Section *Cathayambar* Harms, containing only *Liquidambar formosana* (Fig. 2A), is distinguished pri-

marily by the presence in the pistillate inflorescences of elongate, fleshy, subulate, pubescent setae ("borsten") of varying length, which he interpreted as being "between the female flowers," whereas in section *Euliquidambar* Harms, containing *L. orientalis* and *L. styraciflua* (Fig. 3A), such setae are said to be lacking (H. T. Chang, 1979, also placed *L. acalycina* in this section).

Morphology. The flowers of *Liquidambar* are naked and usually functionally unisexual. They are fused in small, spherical to elongate heads that are spirally arranged in a narrowly conical, complex inflorescence. One to three long-pedunculate, pistillate heads occupy the basal nodes of the inflorescence (Fig. 1A), followed distally by numerous (ca. 15-20) short-pedunculate to sessile staminate heads (Figs. 1A, 4A, staminate portion of the inflorescence, bracts, and stamens removed to show axes). In some inflorescences a pistillate head may be lacking. The staminate and pistillate flowers and heads are usually distinct in form and function, but exceptional and intergrading forms are common. Some examples of such forms are discussed below in a brief consideration of the inflorescence following the morphological descriptions of typical pistillate and staminate flowers.

Pistillate flower. The functionally pistillate flowers are naked but perfect. Six to eight basal or sub-basal, elongate, hyaline bracts subtend the head and initially enclose it but quickly drop off after anthesis. I could find no morphological or anatomical evidence of either a calyx or corolla in any of the primordial or mature flowers examined.

The androecium of the pistillate flower consists of a cycle of five to eight (four to ten in Harms, 1930) stamens inserted at the angles of the floral periphery. The stamens vary in their degree of development from head to head. The anthers may be sessile or borne on short filaments and may range in form from strongly reduced and sterile (Figs. 2A, 3A) to fully developed anthers containing abundant sterile or even fertile pollen. When fertile, however, the anthers apparently do not dehisce until the stigmas of the same flower are well past their receptive period, thus preventing self-fertilization in these proterogynous female inflorescences (Schmitt, 1965).

The gynoecium consists of two (one to six) involute carpels that are fused below but apocarpous above, forming a syncarpous, half-inferior ovary. In the base of the ovary the fused

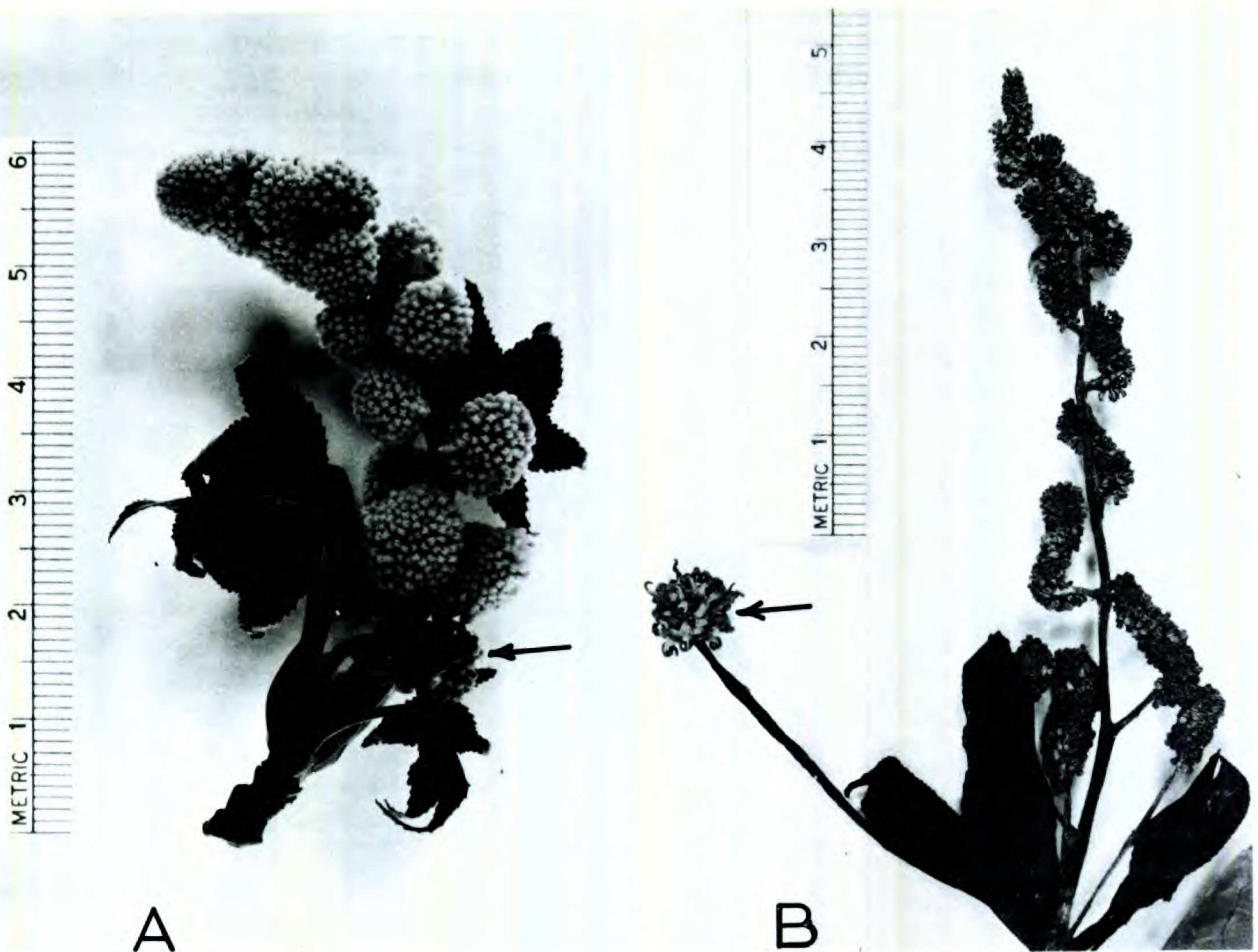


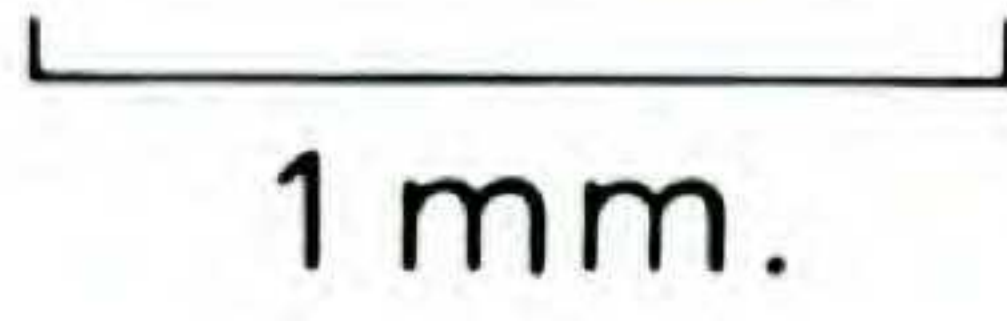
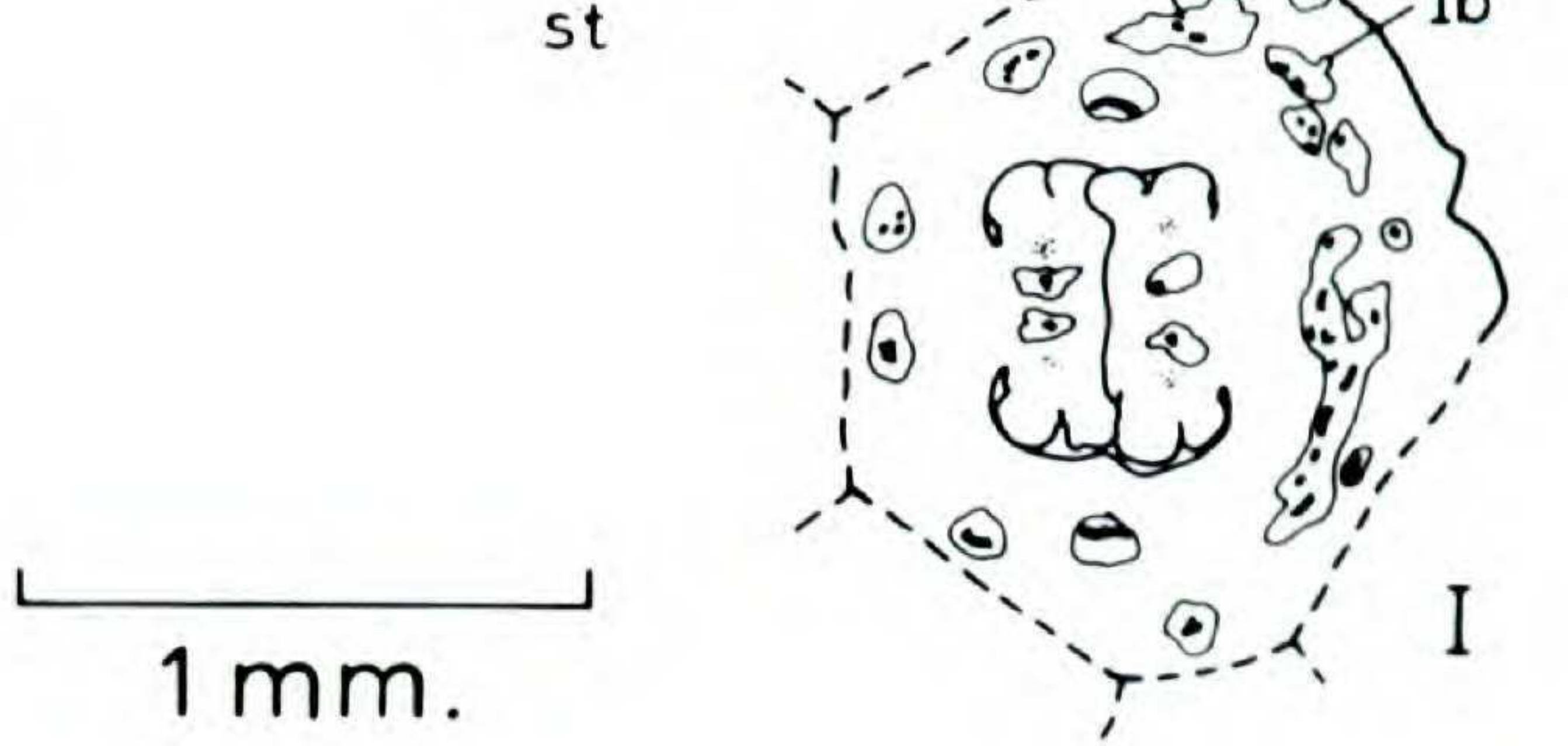
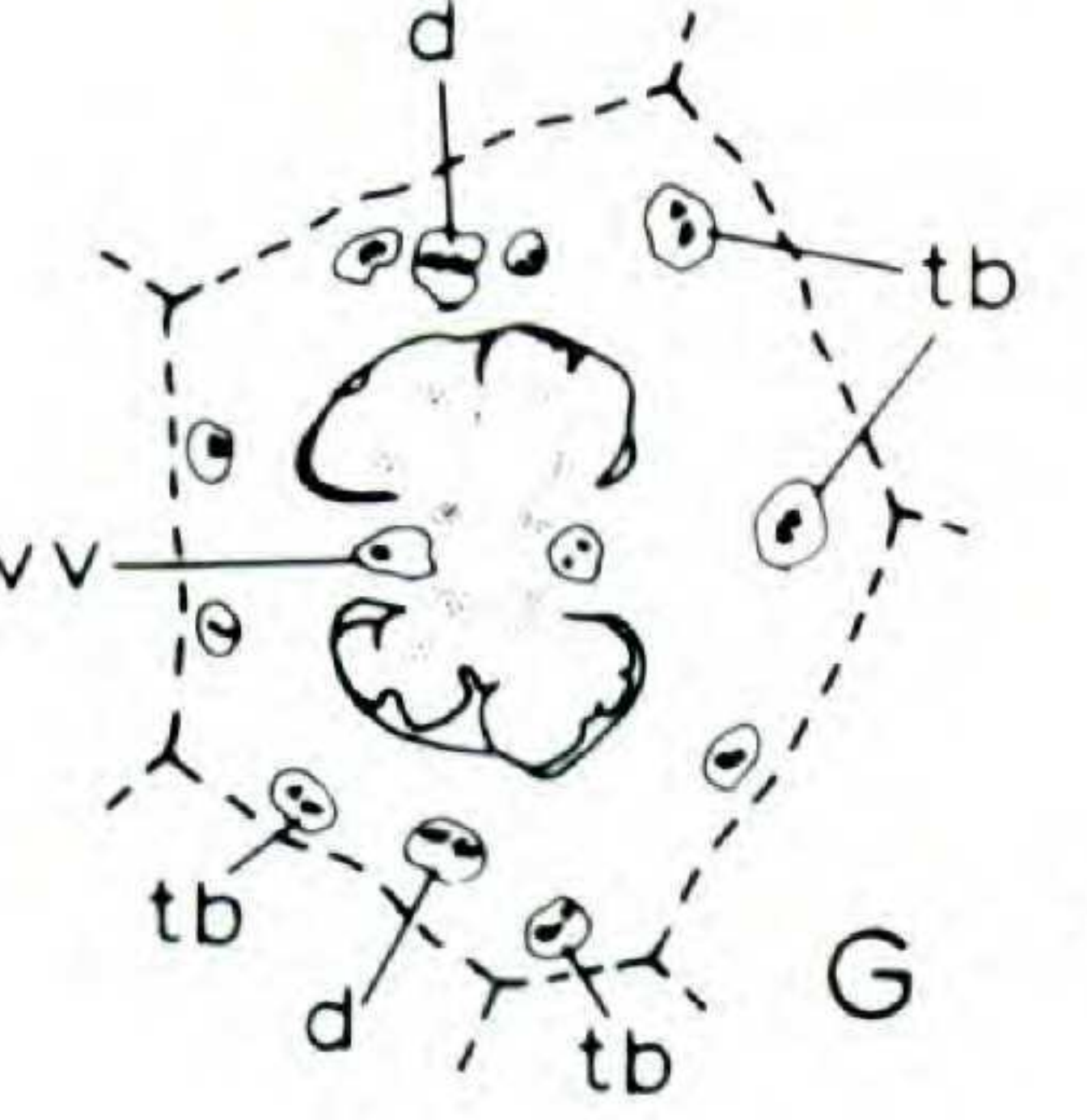
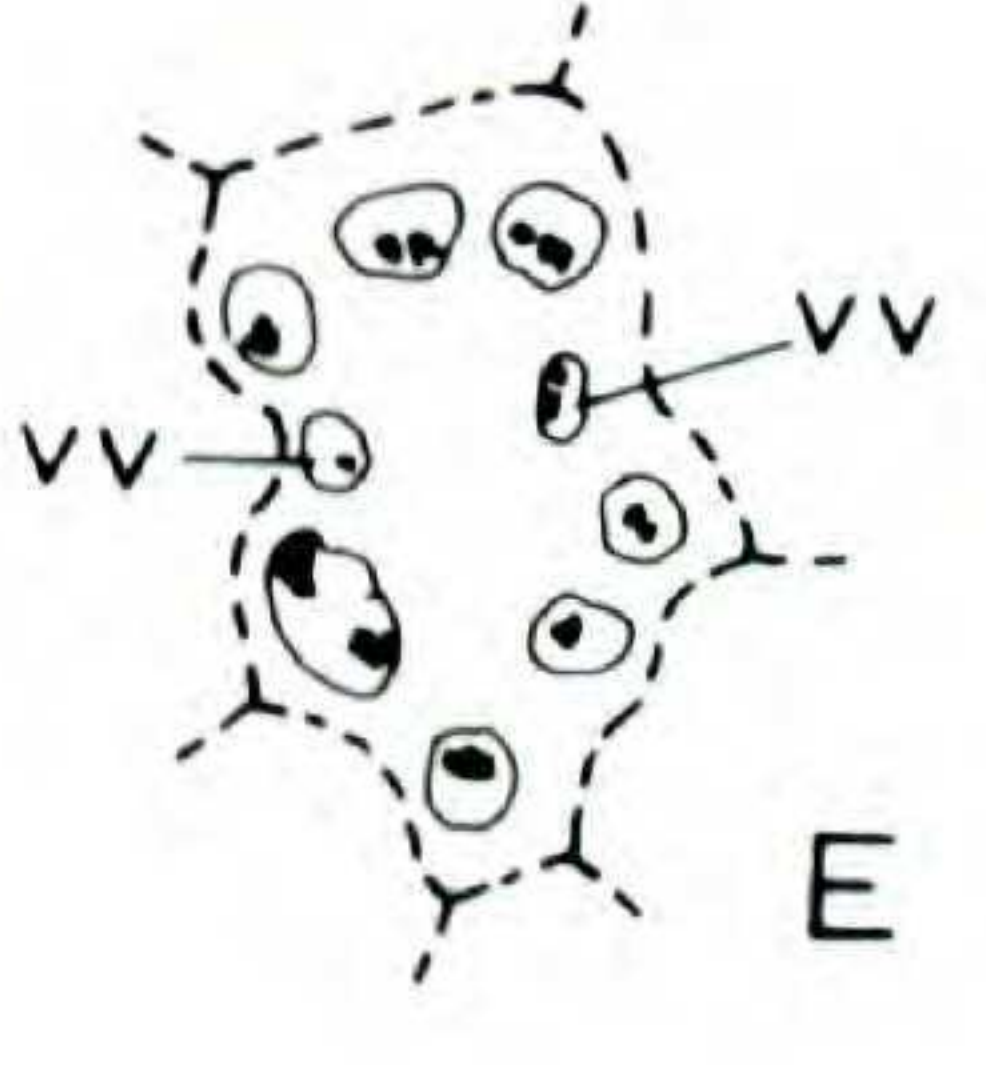
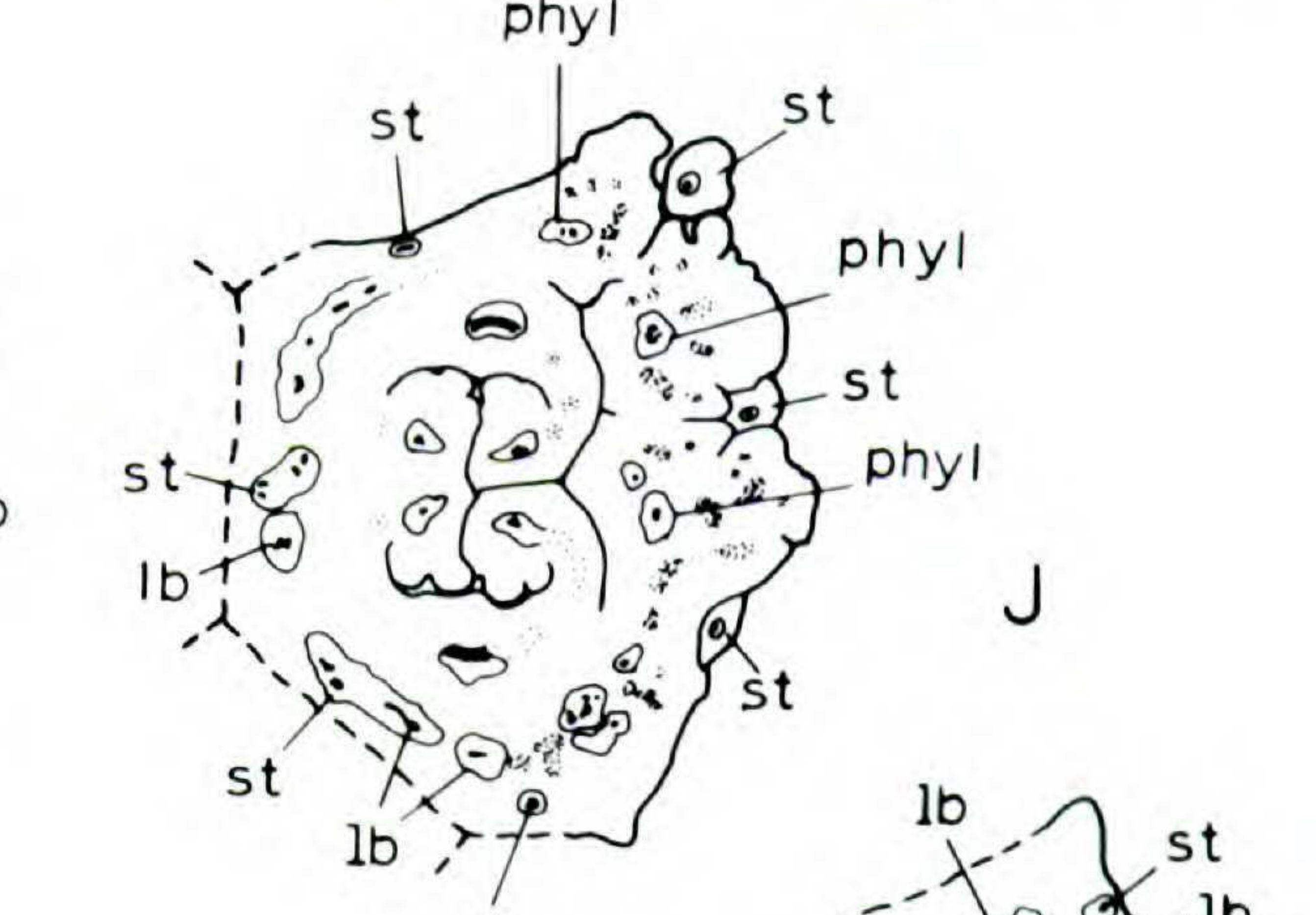
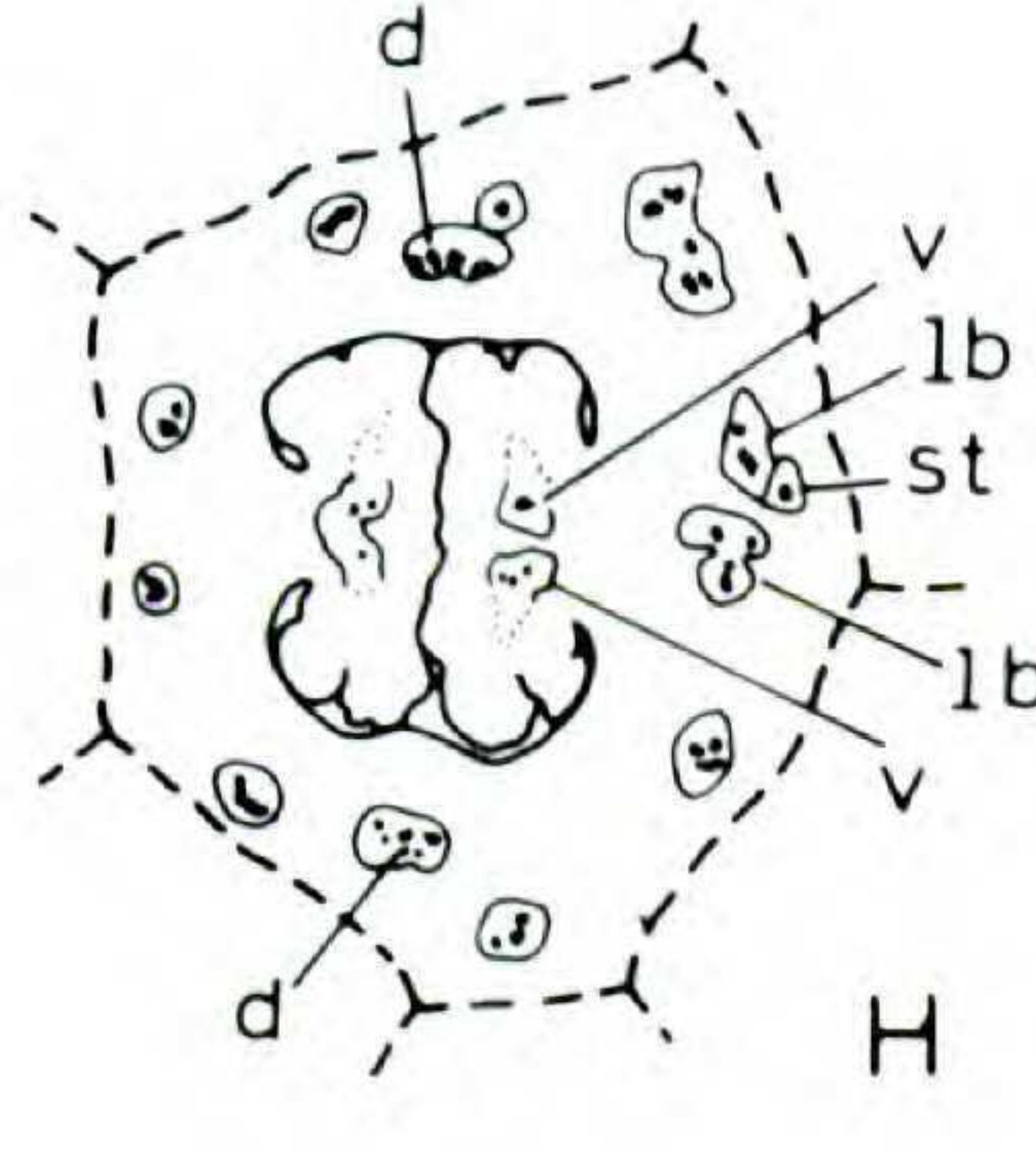
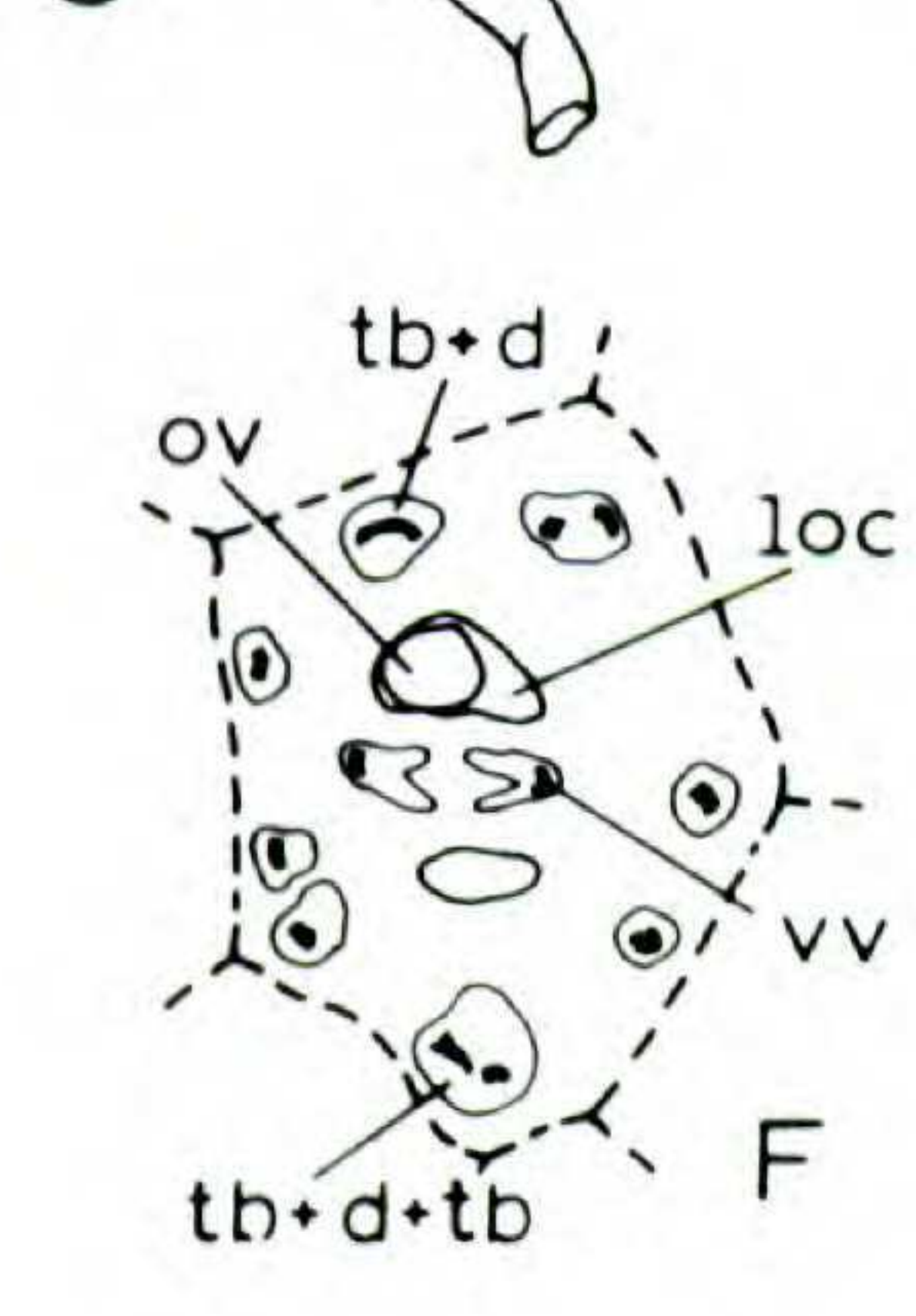
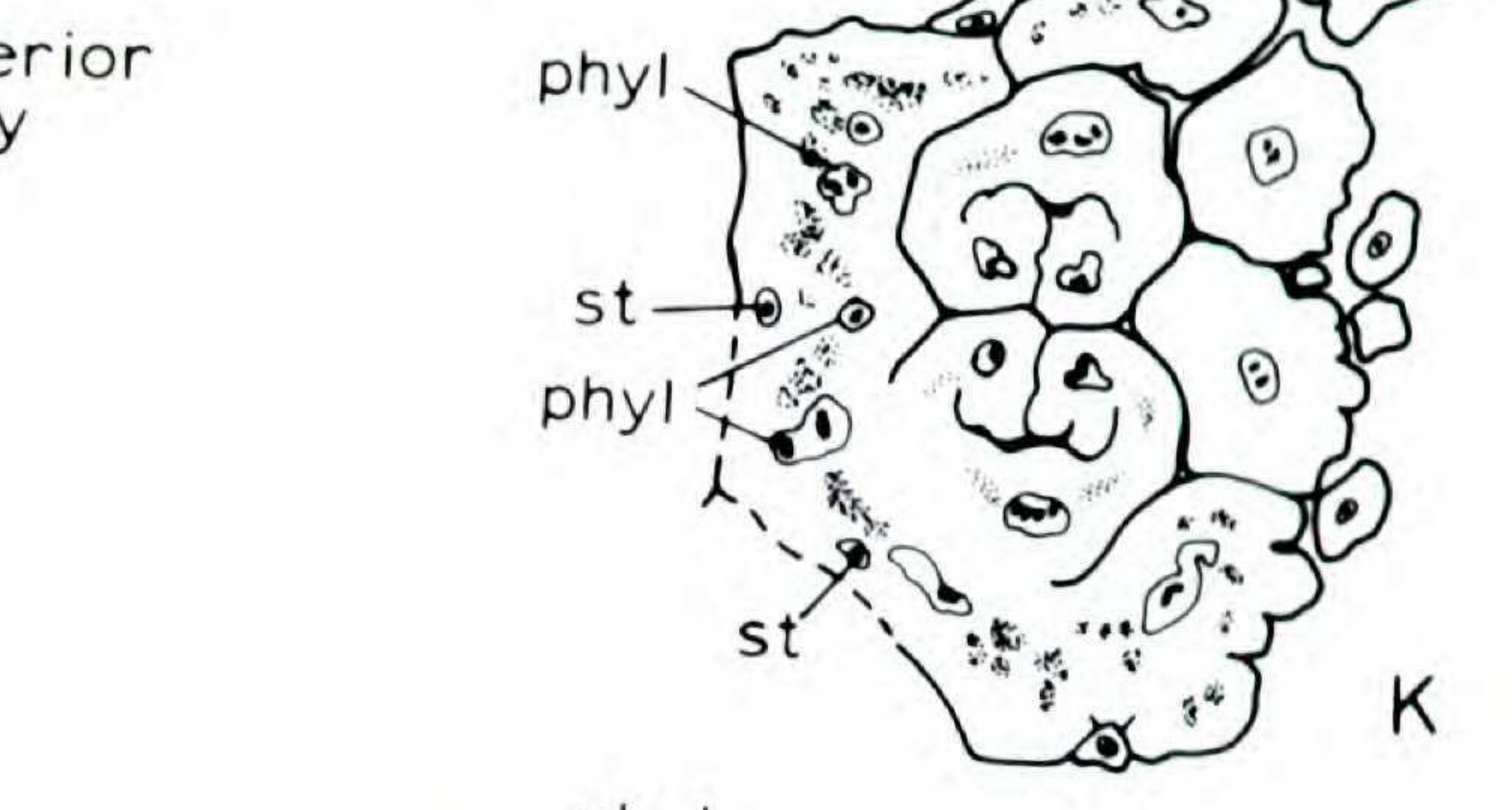
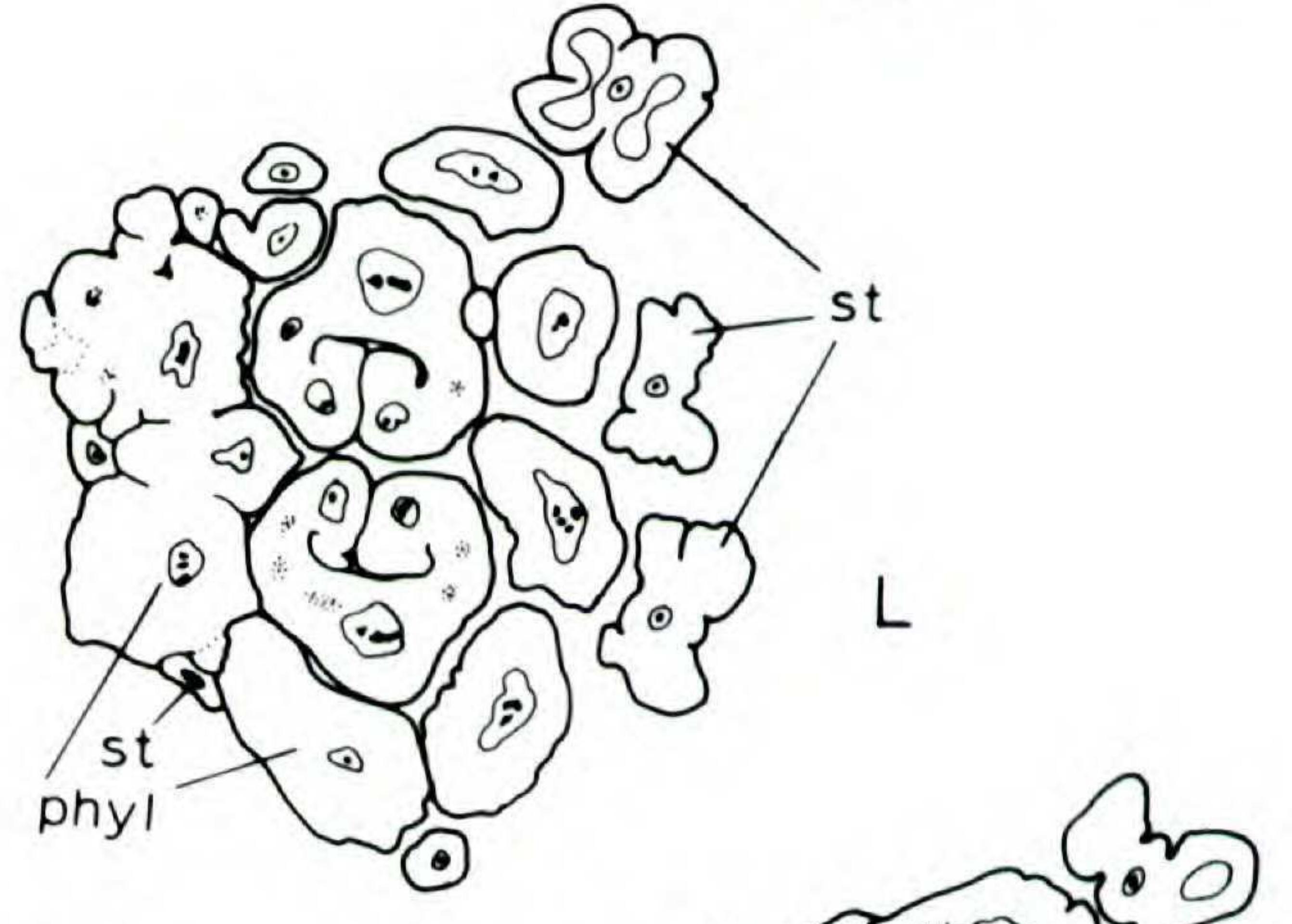
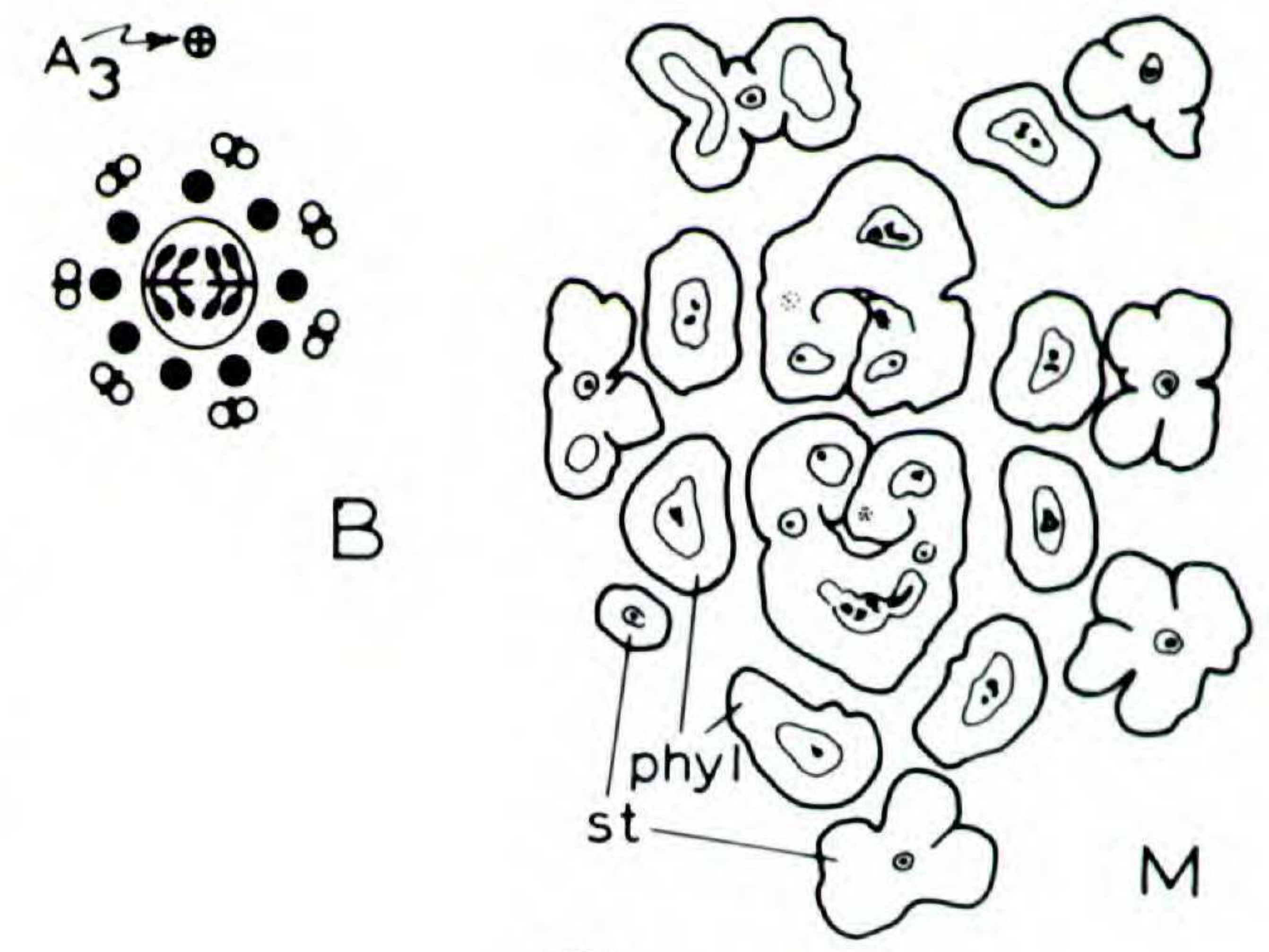
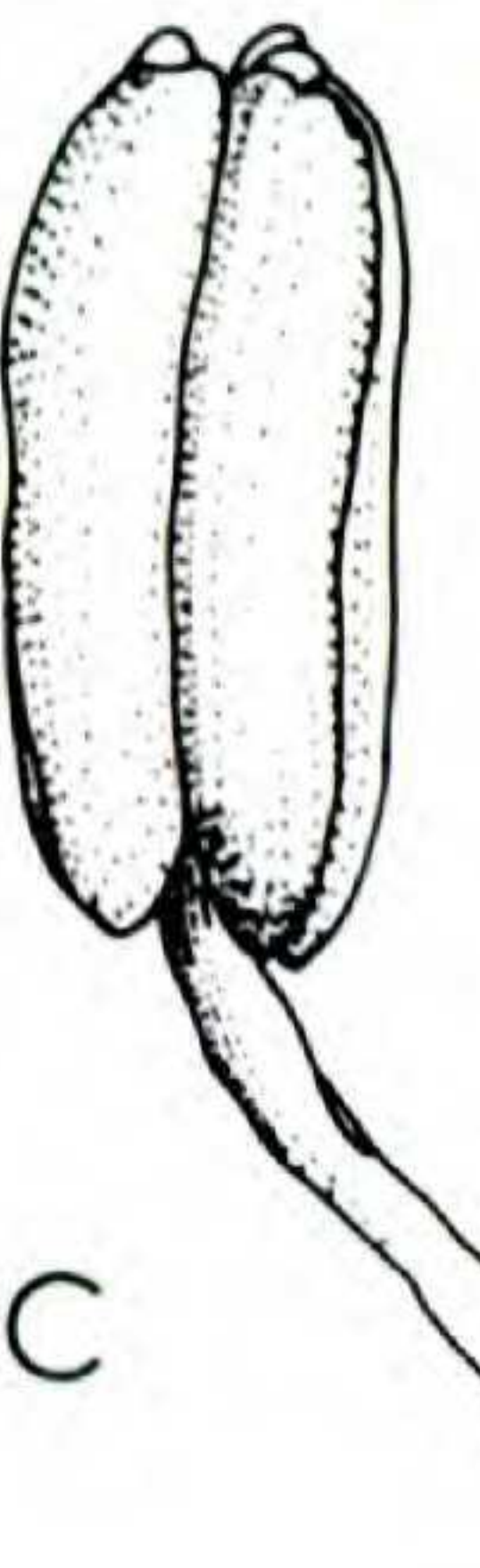
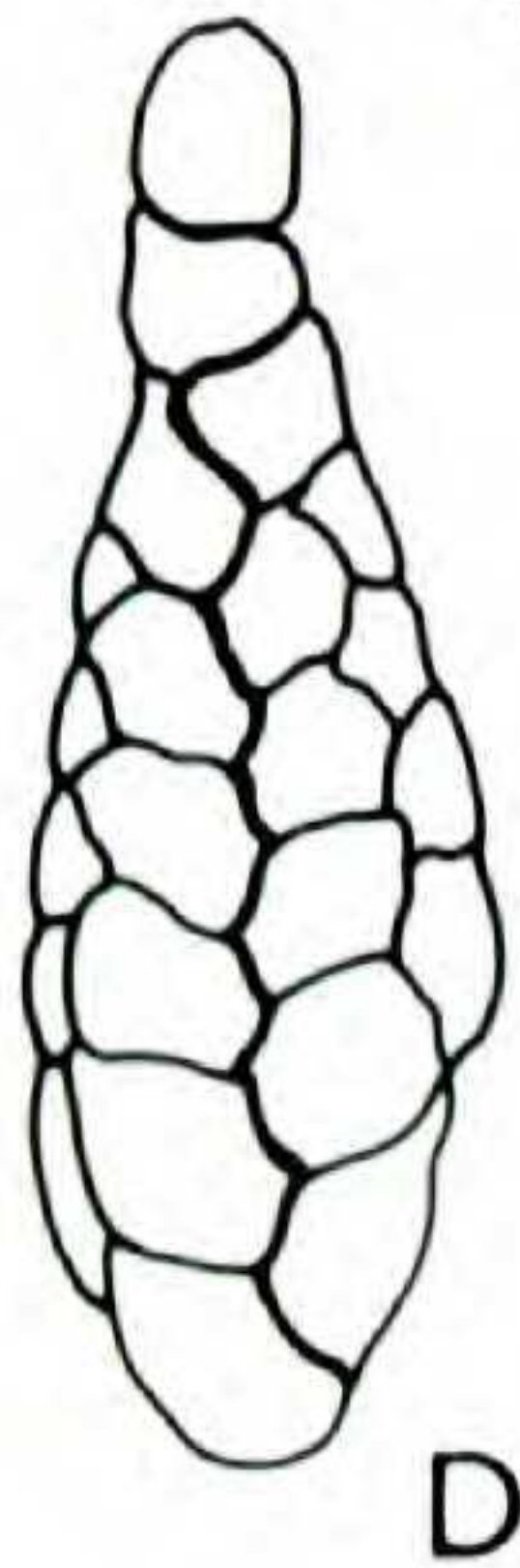
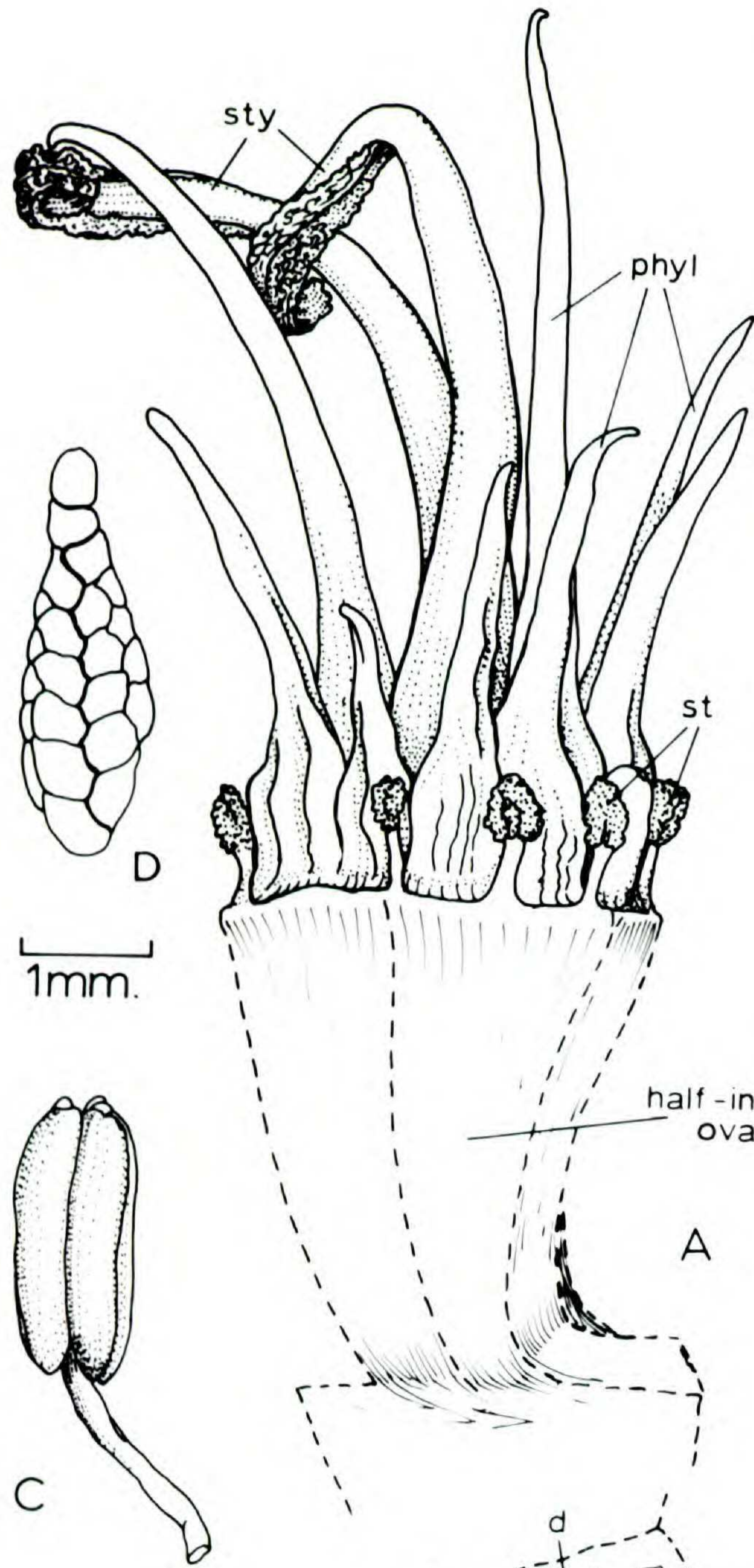
FIGURE 1.—A, B. Total inflorescences of *Liquidambar styraciflua* L. and *altingia chinensis* (Champ.) Oliv. The single, basal, pistillate head in each inflorescence is indicated by an arrow. All other heads are staminate.

carpel margins form a thick but shallow septum (Figs. 2F, G, 3E) that divides a short distance above the base of the locule to form two appressed, compound, parietal placentae (Figs. 2H, 3F, G).

Each carpel margin bears two rows of pendent, anatropous ovules. The number of ovules on each margin in my material ranges from ten to 15 in *Liquidambar formosana* (Bogle 610, Fig. 2D), and ten to 13 in *L. styraciflua* (Bogle 790, 823, "*L. macrophylla*") and *L. orientalis* (Bogle 973). The ovules are arranged in a double row on the central part of each carpel margin, giving way to single ovules above and below (Fig. 2D, see also Griffith, 1836, pl. XVI, as *Sedgewickia*). The ovules of *Liquidambar styraciflua* lack an egg apparatus at the time of pollen release (Schmitt & Perry, 1964). In transverse sections the ovary appears bilocular below but is essentially unilocular above the top of the septum, even though the tightly appressed placentae give the appearance of two locules. Above the septum the tightly appressed carpel margins are not sealed, and the

carpels are thus "open" at pollination. Externally, the dorsal surfaces of the carpels become free from the hypanthium, and adaxially from each other, at a level slightly above the top of the septum (Figs. 2J, K, 3G-I). In the material I studied, the styles of *L. orientalis* and *L. styraciflua* (Fig. 3A) were notably shorter and stouter, and their stigmatic surfaces broader, than those of *L. formosana*, but the possibility of regional variation in style-stigma morphology in these species has not been ruled out.

Surrounding the base of the apocarpous portions of the carpels is a cycle of fleshy, sterile phyllomes (Fig. 2A) that are of particular interest because of the variety of interpretations that have been placed on them by various workers. In *Liquidambar formosana* these take the form of the long setae ("borsten" of Harms, 1930) that characterize section *Cathayambar*. Oliver (1867) described these structures as "long spines, produced from the calyx-limb . . . not at first sight readily distinguishable from the persistent indurated styles." Ek (1902) considered them to



be "isolated perianth parts." Guillaumin (1920) called them "bracteoles" surrounding the female flower, and Harms (1930) suggested that they are vestigial styles of sterile flowers inserted between the fertile flowers. These styliform bodies appear outwardly very much like the functional styles except for their variable size and the absence of stigmatic surfaces (cf. Fig. 2A). The two setae inserted on either side of the ovary in the median plane are usually the largest, perhaps reflecting a slightly greater amount of space for growth and enlargement in the angles between the two carpels. One of these setae is usually larger than its opposite number, often approaching the styles in length. In flowers of *L. orientalis* and *L. styraciflua* these sterile structures are reduced to a cycle of short, blunt, glabrous, fleshy lobes surrounding the carpels ("phyl" in Fig. 3A) and forming the "indistinct—broadly crenate, minutely warty, lobed, protrusive receptacle" described by Harms (1930). Schmitt (1965) described these organs in *L. styraciflua* as "papillae" that "form on the surface of the capsules."

Staminate flower. The naked staminate flowers (Fig. 4) are highly reduced and fused in spirally arranged, congested, bracteate (B_1) spikes, heads, or clusters along the primary inflorescence axis. Each head represents a secondary inflorescence axis (A_2), the larger of which axes, in turn, bear secondary bracts (B_2) with axillary flower clusters (Fig. 4, anthers removed from heads; A, *Liquidambar styraciflua*; B–F, *L. orientalis*). The staminate flowers may be strictly staminate or contain the merest vestiges of rudimentary carpels [Fig. 4B(5), note the partially developed styles and stigmas of several ovaries; 4C(3) and 4F, note tips of rudimentary carpels visible within cycle of stamens]. Each flower contains four to eight (to ten) stamens arranged in a single cycle, although the flowers and stamens are often so

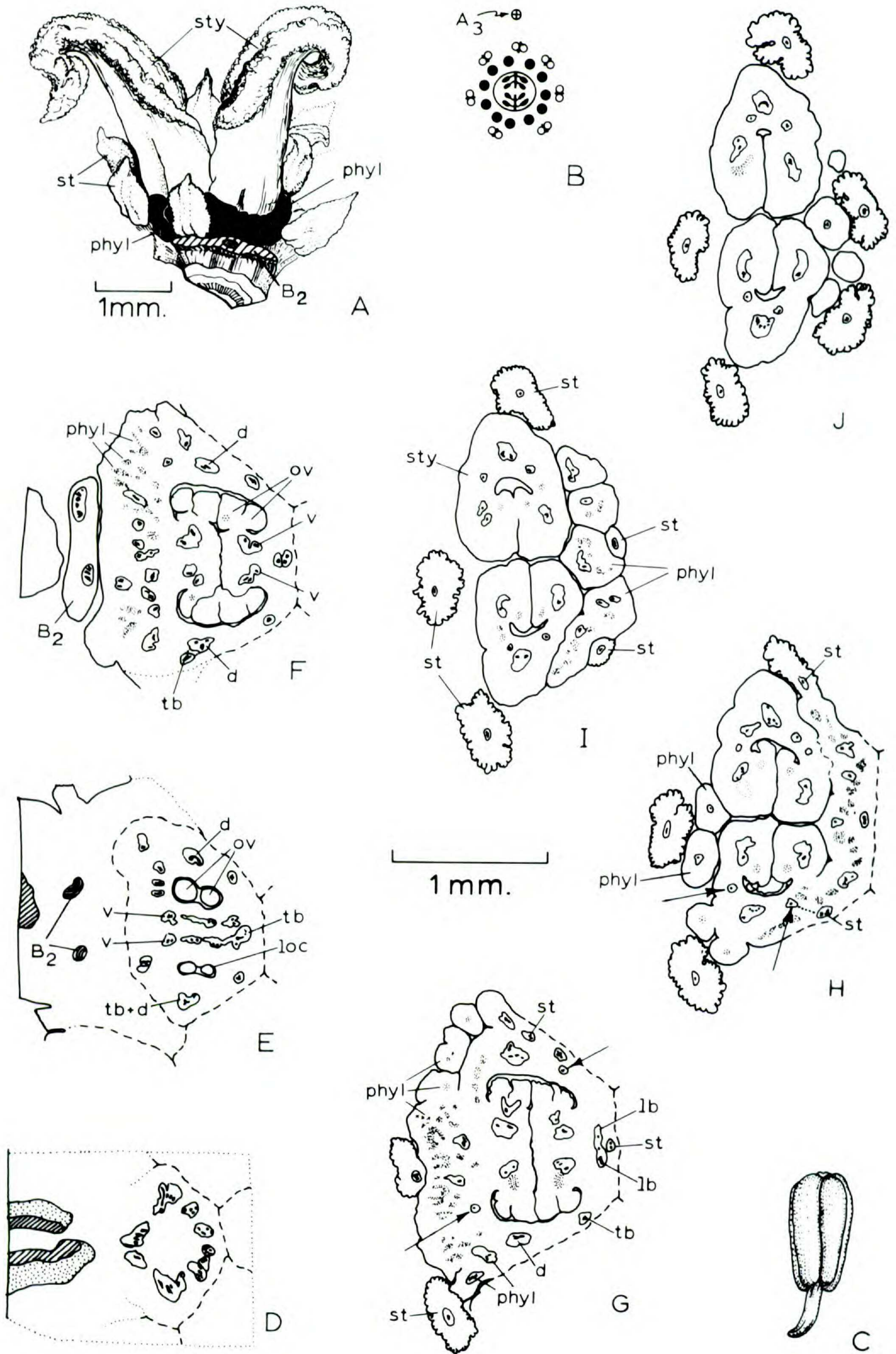
densely crowded that it is sometimes difficult to determine this detail of floral structure. I found no evidence in *L. orientalis* to support Ek's (1902) statement that each staminate flower consists of one stamen. There is no evidence in the typical staminate flower of the cycle of sterile phyllomes that is so prominent in the pistillate flower.

Near the base of each staminate head distortion of the flowers, due to such factors as reduction of the peduncle, fusion of the peduncle to the primary inflorescence axis, and differential growth, make it difficult, if not impossible, to delimit individual flowers. In the middle and distal portions of the head, however, it is often apparent that the stamens are arranged around shallow, pubescent, elongate pits or depressions in the surface of the axis [Fig. 4C(3)]. The pubescent tips of two abortive carpel primordia are frequently visible within the ring of stamens at either end of the pit. Tong (1930, fig. 10) noted such vestigial gynoecia in male flowers of *Liquidambar formosana*.

The mature fertile stamens (Figs. 2C, 3C) contain four sporangia and dehisce by means of two simple, lateral, longitudinal slits. At anthesis the pistillate heads are pendent on long peduncles, whereas the main axis of the total inflorescence, bearing the staminate heads, is more or less erect. After pollination the entire distal staminate portion of the inflorescence (Fig. 4A) quickly withers and drops away. The peduncles of the pistillate heads remain attached and the heads ripen and enlarge several-fold. Most of this enlargement is due to the growth of the numerous ovaries within the head, but part of it is apparently attributable to the activity of a vascular cambium in the axis of the head (Schmitt, 1965). The seeds are shed in the fall.

Inflorescence variation. Although staminate and pistillate heads are usually strongly differ-

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 FIGURE 2. *Liquidambar formosana* Hance. —A. Pistillate flower at anthesis, excised from a head. —B. Floral diagram. —C. Stamen from a staminate flower. —D. Arrangement of ovules on margins of one carpel. E–M. Serial sections of a pistillate flower at anthesis, cut slightly obliquely. —E. Through the receptacle; several trunk bundles and two compound ventrals visible. —F. Bases of locules; compound ventral bundles formed. —G. Through lower part of locules, showing ovule traces departing from compound ventrals. —H. Through ovary; the compound ventral bundles dividing. —I. Through ovary; approaching top of the inferior portion; trunk bundles branching to form traces to stamens, phyllomes, and carpels. —J. Partial separation of the hypanthium from the ovary; insertion of some stamens and phyllomes; procambial strands of phyllome supply stippled here. —K. Carpels free of each other adaxially; hypanthium nearly free. —L. Insertion of remaining stamens and phyllomes. —M. Through the style bases, anthers, and phyllomes. (Key: A_3 , tertiary axis; d, dorsal carpel bundle; lb, lateral branch; loc, locule; ov, ovule; phyl, phyllome; st, stamen, stamen trace; sty, style; tb, trunk bundle; v, ventral carpel bundle; vv, compound ventral bundle.)



entiated, unusual variations in inflorescence structure have frequently been observed and are also reported in the literature. On several occasions I have seen inflorescences of *Liquidambar styraciflua* and *L. orientalis* in which the flowers of the lower staminate heads contain partially developed but sterile gynoecia. Various degrees of development of the gynoecium among staminate flowers in a single head of *L. orientalis* are illustrated in Figure 4B, C. For the sake of clarity in these drawings the secondary bracts subtending the individual flowers or axillary floral clusters in the head have been removed (indicated by hatched areas), as have the anthers. In addition, each axillary group of flowers is illustrated in diagrammatic form to the left of the drawings. The secondary bracts are numbered in ascending order on the axis. Each stamen is represented in the diagrams by a small circle, a rudimentary ovary by an ellipse, and the absence of an ovary by a cross. Figure 4B(1) and 4E illustrate a single staminate flower consisting of seven stamens and lacking any external evidence of a vestigial ovary. This flower is seen in lateral view in Figure 4C(1), and diagrammatically in Figure 4E. Figure 4C(3) shows a secondary bract with a single, axillary, staminate flower that contains two rudimentary carpels surrounded by nine stamens (cf. diagram in Fig. 4F). The tips of the two abortive carpel primordia are apparent at either end of a minute pit in the center of the flower. Figure 4B(5) illustrates an axillary complex of seven staminate flowers of which five contain partially developed ovaries and styles, while two contain no ovaries. Although quite crowded on a short, conical axis, the limits of each flower could be ascertained by studying the placement and orientation of the stamens. Where two or three flowers abut, the stamens may occur in tufts of three or four. The composition of the

seven flowers in the complex is shown diagrammatically in Figure 4D. The presence within a single staminate head of several secondary bracts with associated axillary floral clusters indicates clearly that each head of the inflorescence is a reduced branch system containing axes of at least two orders (secondary and tertiary) in addition to the floral pedicels and points up the complexity of the inflorescence in the subfamily.

Inflorescences of *Liquidambar styraciflua* in which all heads are developed to the pistillate state were reported by Britton (1887) and illustrated by Kirchheimer (1947). I have seen inflorescences in this condition on trees in the Arnold Arboretum and University of Washington Arboretum (Seattle), as well as on trees obtained from commercial sources and on native trees in eastern Pennsylvania. Such inflorescences are unusual but not rare and may be considered as concrete evidence of the bisexual potential of the staminate flowers of *Liquidambar*. Inflorescence variation of this type has also been observed in *Altingia*.

Although functionally pistillate, the female flowers normally contain stamens that are reduced and sterile. However, I have observed pistillate heads of *Liquidambar formosana* in which the stamens vary in development from tiny, clavate staminodia, as in Figure 2A, to fully developed stamens containing abundant pollen. The absence of a staining reaction with lactophenol-aniline blue, however, suggested that this pollen was not viable. Similarly, Shoemaker (1905) reported abortive pollen, and Schmitt (1965) reported viable pollen in the anthers of pistillate flowers of *L. styraciflua* in New York and North Carolina, respectively.

Floral vascular anatomy. In the following paragraphs the floral vasculature of *Liquidambar formosana* is first described in detail. The pat-

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FIGURE 3. *Liquidambar styraciflua* L.—A. Pistillate flower at anthesis; one of the basal flowers in a head, with subtending secondary bract.—B. Floral diagram.—C. Stamen from a staminate flower. D–J. Serial sections of a pistillate flower at anthesis, cut slightly obliquely.—D. Through the receptacle, showing several large bundles.—E. Bases of locules; ventral bundles forming.—F. Through lower part of the ovary, showing branching trunk bundles on left; separation of placentae; traces to ovules departing from the ventral bundles.—G. Through the upper part of the inferior portion of the ovary; arrows indicate supplementary bundles to the carpel walls derived from trunk bundles.—H. Separation of the carpels; traces to stamens and phyllomes on the right side; procambial vasculature of the phyllomes stippled.—I. Insertion of the stamens and phyllomes on the right.—J. Through bases of styles, papillate anthers of sterile stamens. (Key: A₃, tertiary axis; B₂, secondary bract; d, dorsal carpel bundle; lb, lateral branch; loc, locule; ov, ovule; phyl, phyllome; st, stamen, stamen trace; sty, style; tb, trunk bundle; v, ventral carpel bundle.)

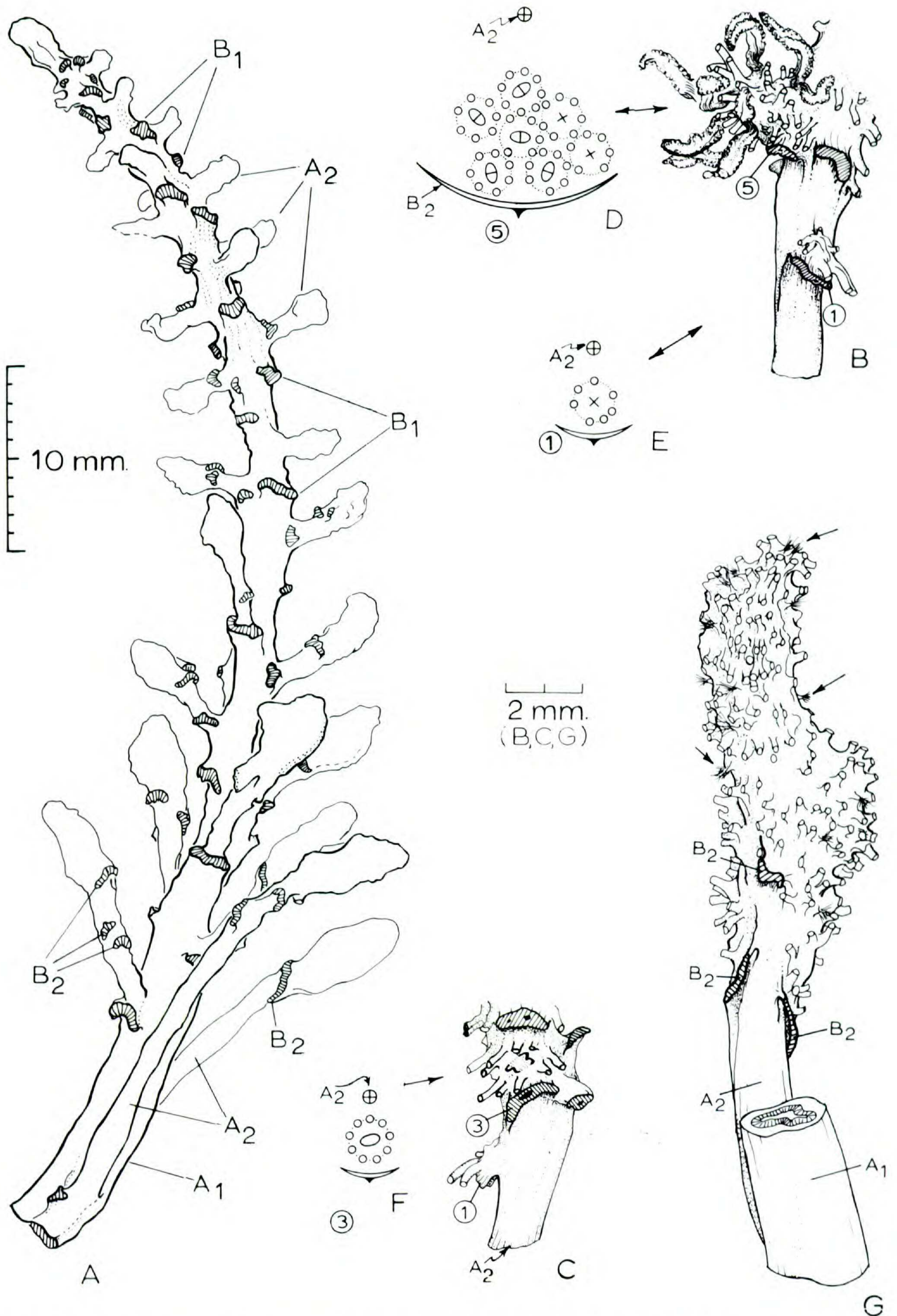


FIGURE 4. Staminate partial inflorescences of *Liquidambar styraciflua*, *L. orientalis*, and *Altingia chinensis*. — A. The staminate portion of the total inflorescence of *L. styraciflua* after anthesis, with all anthers removed, showing central primary axis with primary bract scars, and secondary axes with secondary bract scars. B, C. Portions of secondary axes of the staminate partial inflorescence of *L. orientalis*, showing various stages of

terns of the other two species are then described to the extent that they differ from that of *L. formosana*.

Pistillate flower. A typical pistillate flower of *Liquidambar formosana*, excised from a head, is illustrated in Figure 2A. At anthesis the major vascular features of the flower are discernible even though some of the vasculature is only procambial in those portions of the flower that later undergo considerable enlargement and development (e.g., the ramifying bundle systems in the cycle of phyllomes, or the vascular network of the carpel walls).

The vascular supply to the flower is variable. As many as ten bundles enter the base of the sessile flower from the peduncular stele (Fig. 2E). In the receptacle these rapidly give rise to a peripheral system of five to eight trunk bundles (tb), which eventually supply the stamens, the phyllomes, and the carpels as an inner series of four ventral (v) and two dorsal (d) carpel bundles (Figs. 2F–H, 6I). There is also considerable variation in the organization of the dorsal and ventral bundles. A dorsal bundle may be formed in the ovary wall by the radial or tangential division of a trunk bundle; through the fusion of two lateral branches from adjacent trunk bundles; or directly by one of the bundles entering the receptacle from the peduncular stele. Except in the last case the formation of the dorsals occurs at varying levels in different carpels.

The ventral bundles originate from the receptacle below the base of the locules. The ventrals of adjacent fused carpel margins may originate individually as branches from trunk bundles, or they may be united in a compound ventral bundle (vv) in the base of the ovary (Fig. 2E, F). If united basally, the individual ventrals (v) become distinct in the septum a short distance above the bases of the locules (Fig. 2G, H).

The peripheral trunk bundles (tb) ascend in the wall of the hypanthium to supply the stamens and phyllomes. At the base of the androecium

each trunk bundle branches tangentially. The abaxial branch supplies a single trace (st) to the base of a sterile stamen (Fig. 2H–J). The adaxial branch then divides to form two to three branch traces (phyl), which supply the bases of adjacent phyllomes. If a single large phyllome occupies the position between two adjacent trunk bundles (or sterile stamens), its base may receive traces from each of the adjacent trunk bundles. If two smaller phyllomes occur between two trunk bundles, each will receive one or more traces from each of the nearest trunk bundles. The traces ramify extensively in the fleshy base of the phyllome, forming an ascending system of bundles (indicated by stippling in Fig. 2J, K). At higher levels in the phyllome only a single prominent central bundle persists (Fig. 2K, L), ascending to the tip of the phyllome, as has been noted also by Schmitt (1965). In transverse sections the bases of the phyllomes often appear lobed and divided (Fig. 2J, K), and the larger lobes, at least, may be supplied by procambial strands at anthesis. The secretory ducts that accompany the vascular bundles throughout the plant are also present in the bundle systems of the phyllomes. At the level of separation of the carpels from the phyllomes (Fig. 2J–L), it often appears that the stamen and phyllome bases remain fused for a very short distance, as if in a floral tube. This may or may not represent the vestige of a hypanthial tube. This condition is occasionally present in *Liquidambar styraciflua* as well.

The dorsal carpel bundles pass upward and, in the apocarpous portion of each carpel, produce at least two pairs of subopposite secondary branches that move upward and toward the carpel margins, where they fuse with the ventral bundles. Transverse sections may thus show four to seven bundles in the carpel wall (Fig. 2L, M).

The ventral carpel bundles (vv, v) ascend through the septum and into the placentae (Fig. 2F, H, I). Traces to the ovules are produced in both the septum (Fig. 2G) and in the free com-

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gynoecial development in staminate flowers.—B. Secondary bract (5), with axillary complex of seven flowers, several of which contain partially developed gynoecia. Compare with the diagrammatic presentation at D. Secondary bract (1), with a single axillary flower with seven stamens, no gynoecium. Compare with diagram at E.—C. Secondary bract (3), with a single axillary flower containing eight stamens and two abortive carpel primordia at either end of a central depression (stippled). Compare with diagram at F.—D–F. Diagrammatic representations of the flowers illustrated at B and C.—G. The clavate secondary axis of a single staminate head from an inflorescence of *Altingia chinensis*. Pubescent vestigial carpel primordia indicated by arrows. (Key: A₁, primary axis; A₂, secondary axis; B₁, primary bract; B₂, secondary bract; circled numerals designate bracts and associated axillary flowers.)

pound placentae (Fig. 2H, I); placentation is thus axile below, but parietal above. In the distal portion of the ovary the ventrals produce an occasional minor branch to the carpel wall before passing into the style bases.

The vascular anatomy of the female flowers of *Liquidambar orientalis* and *L. styraciflua* (Fig. 3) is essentially like that of *L. formosana*. The origins of the dorsal and ventral bundles of the ovaries of these species are fully as variable as in *L. formosana* (cf. Fig. 3D–F). An interesting deviation, however, is the adnation in these two species of a lower pair of carpel secondary veins to nearby trunk bundles of the hypanthium. Each of these secondary bundles originates below the level of separation of carpel from hypanthium, arising as a branch from a trunk bundle (or one of its major branches) on either side of the dorsal bundle (arrows, Figs. 3G, H, 6D). They move adaxially into the carpel wall and eventually fuse with adjacent ventral bundles.

In *Liquidambar styraciflua* (Bogle 823) the ventral bundles may appear slightly diffuse (Fig. 6A, B), with some of the strands diverging to form ovule traces while others ascend into the style bases. In other cases the ovules may be supplied from a branch of the ventral that dies out after supplying traces to the ovules.

The ramifying bundle system that vascularizes phyllomes, as seen in cleared specimens of *Liquidambar styraciflua*, varies from quite complex (Fig. 6C, Bogle 823) to relatively simple (Fig. 6D, Bogle 790). In scanning electron micrographs widely scattered stomata can be seen in the epidermis of both the phyllomes and carpels of *L. styraciflua*.

Staminate flower. Typical staminate flowers in all three species are highly modified (Fig. 4B, C), and the vasculature of their receptacles and axes is very diffuse and complex. In cleared staminate heads individual flowers are barely or not at all discernible on the basis of vasculature alone. Stamen bundles radiate from the margins of gaps in a loosely expanded peduncular stele. Each gap appears to correspond to a single flower, but gaps may become confluent, forming large open spaces in the stele. A bundle emanating from the margin of a gap may: supply a single stamen base directly; divide to form two traces to separate stamens; or anastomose with a second bundle to form the supply to one stamen. I found no evidence of a vascular supply to any of the abortive carpel primordia mentioned above and illustrated in Figure 4. But it would not be surprising

to find such a supply in staminate flowers with partially developed gynoecia, such as those of *Liquidambar orientalis* illustrated and diagrammed in Figure 4B(5) and 4D.

2. **Altingia** Noronha, Verh. Batav. Genootsch. Kunsten 5(2): 1. 1790. Figures 1B, 4G, 5, 6E–J.

About seven to 14 species are currently recognized in the genus *Altingia* (Vink, 1957; Tardieu-Blot, 1965; H. T. Chang, 1962, 1973, 1979). The genus is distributed from Bhutan and Assam eastward to southern China, and southward through Malaya to Java and Sumatra. In their natural state the massive, evergreen trees of *Altingia* may achieve heights of up to 60 meters, prompting their description as the kings of the mountain forests in southeast Asia, particularly in Indonesia.

The evergreen leaves of *Altingia* are simple to pinnately-lobed, stipulate, with an entire or serrate margin. They contrast sharply in form with the deciduous, palmately-lobed and -veined leaves of *Liquidambar*. However, intermediate leaf forms, and conditions of persistence, are described in the species attributed to the segregate genus *Semiliquidambar* H. T. Chang (1962, including *A. chingii* Metc. as *Semiliquidambar chingii*, and four new species, since reduced to three by H. T. Chang, 1979).

Morphology. Inflorescences of *Altingia* are terminal on vegetative axes, and appear to be basically similar to those of *Liquidambar* in composition, with a comparable range of variation. The staminate heads are often more elongate and oblong in appearance than those of *Liquidambar* (Fig. 1), and the internodes and peduncles are often longer, giving the total inflorescence a longer, looser appearance. The majority of herbarium specimens seen bear only older pistillate heads; very few bear anthesis stage or young inflorescences that permit observations of the total inflorescence. This problem is noted by Tardieu-Blot (1965) in her treatment of the six species of *Altingia* occurring in Cambodia, Laos, and Vietnam. In fact, flowers are listed as unknown for five of the six species she describes. Vink (1957) described the inflorescences of Malaysian *Altingia* in part as: "male heads in racemes consisting of masses of stamens, intermingled with some minute ?bracts," and "female heads solitary, in racemes or in the lower part of male racemes."

Young inflorescences containing at least one

pistillate head at the basal node, with numerous distal nodes bearing pedunculate to sessile staminate heads, have been observed in herbarium specimens (GH, A) of *Altingia chinensis* (Champ.) Oliver, *A. excelsa* Nor., *A. gracilipes*, and *A. obovata* Merr. & Chun. Some inflorescences of *A. chinensis* have two or three pistillate heads at the basal nodes. In contrast, unisexual inflorescences of *A. excelsa* containing 11–16 pistillate heads arranged in a narrowly conical fashion occur in specimens of *Abbe 10298* in my collections. In these, the lower heads are pedunculate, the intermediate and upper heads grade from short-pedunculate to sessile, whereas the two or three most distal heads are fused in a terminal mass.

The number of flowers in each pistillate head varies among the species of *Altingia* from numerous (in excess of 25) to as few as six. In fruit this results in heads that range in shape from globose in species such as *A. chinensis* or *A. yunnanensis*, to obovate or obpyramidal in *A. takhtajanensis* and *A. siamensis* (compare illustrations in Tardieu-Blot, 1965, pl. IV, V). This contrasts with the many-flowered pistillate heads of *Liquidambar*, which are typically globose.

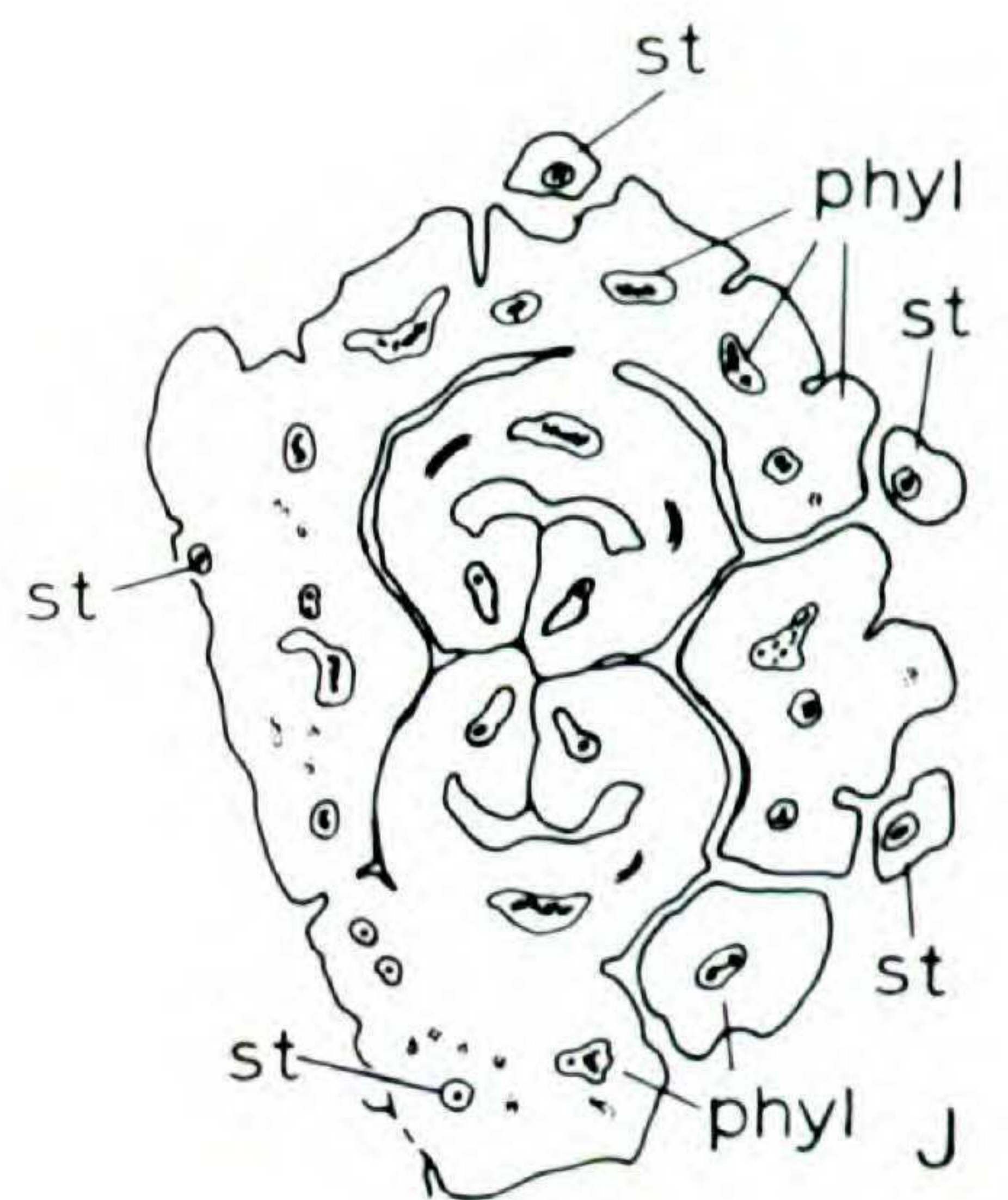
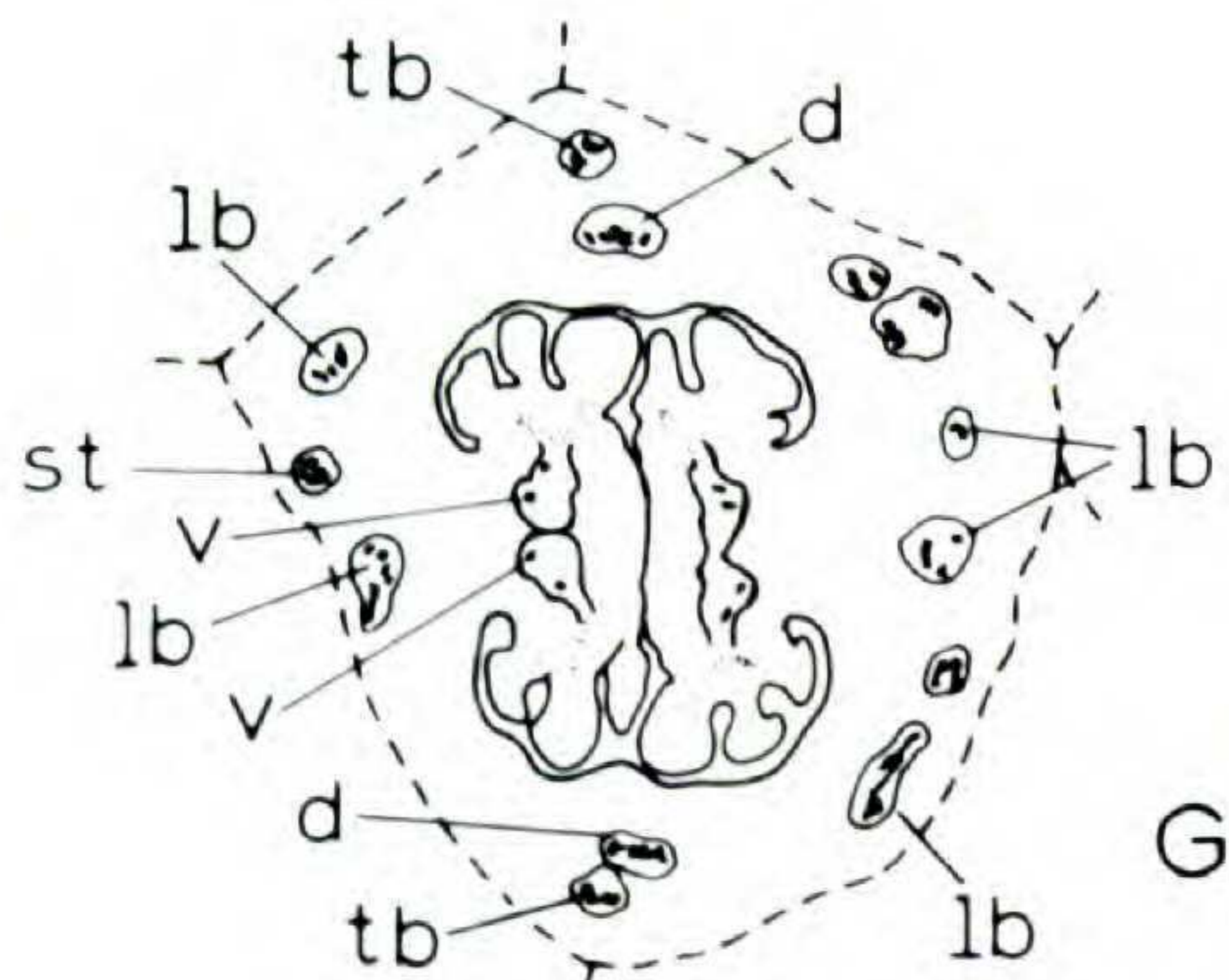
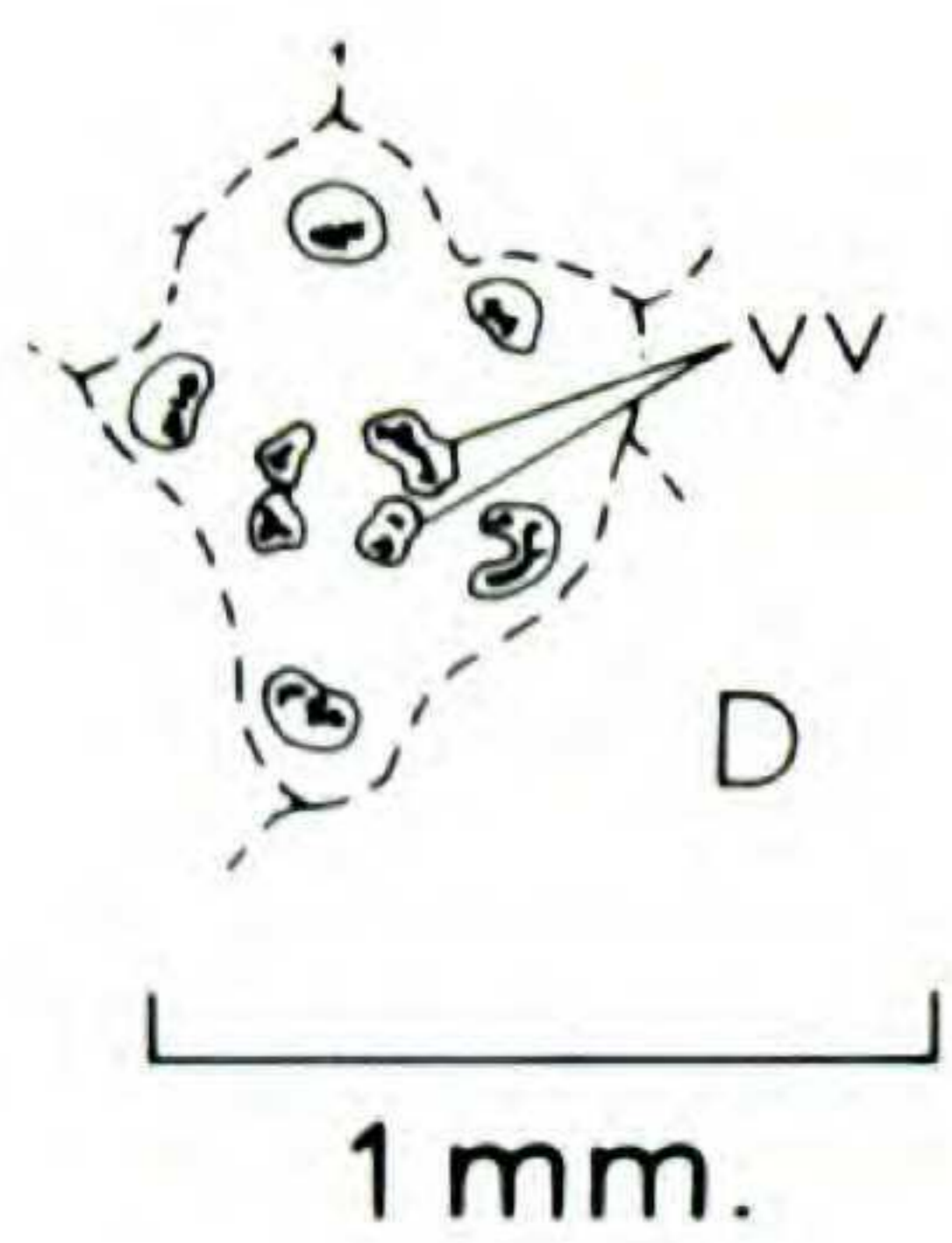
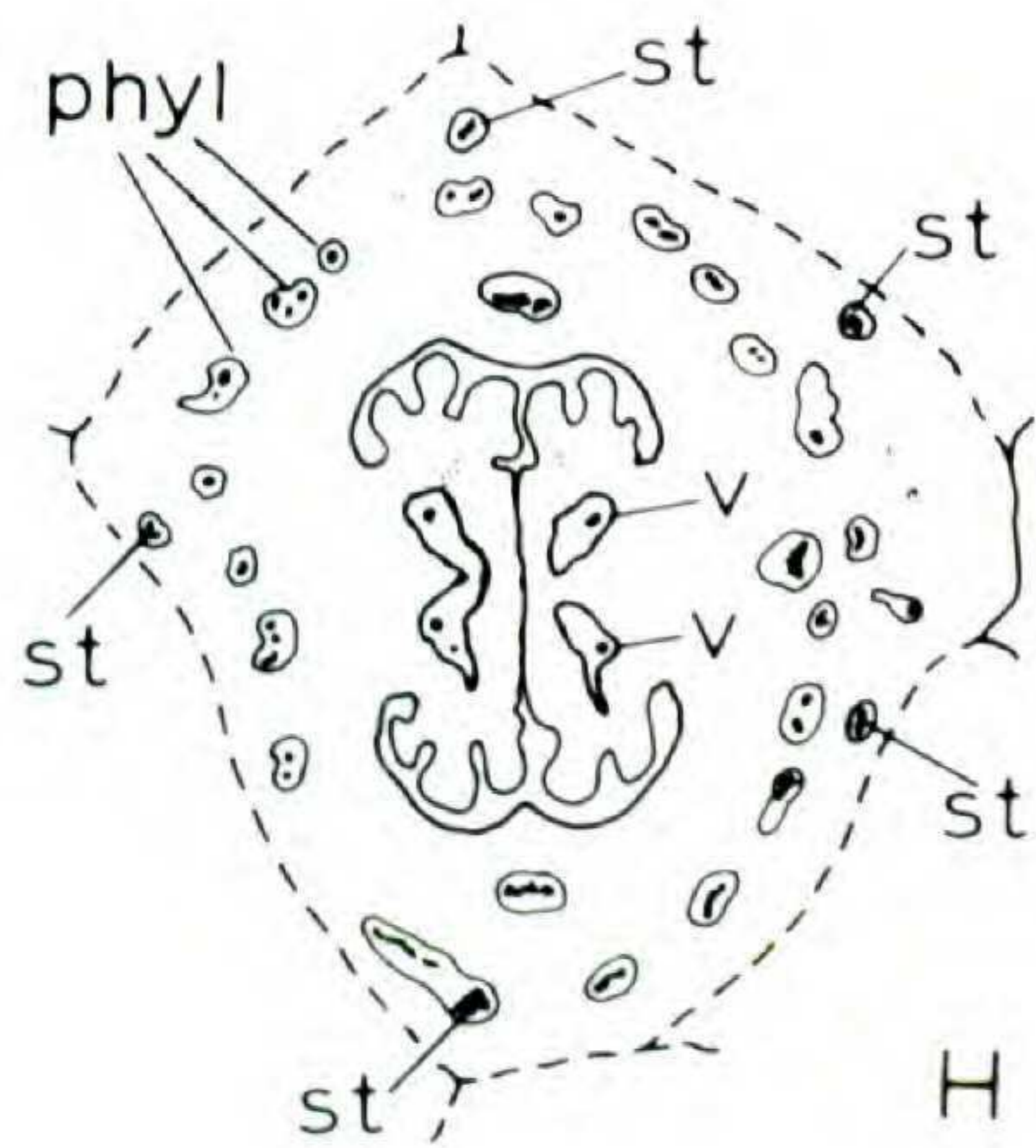
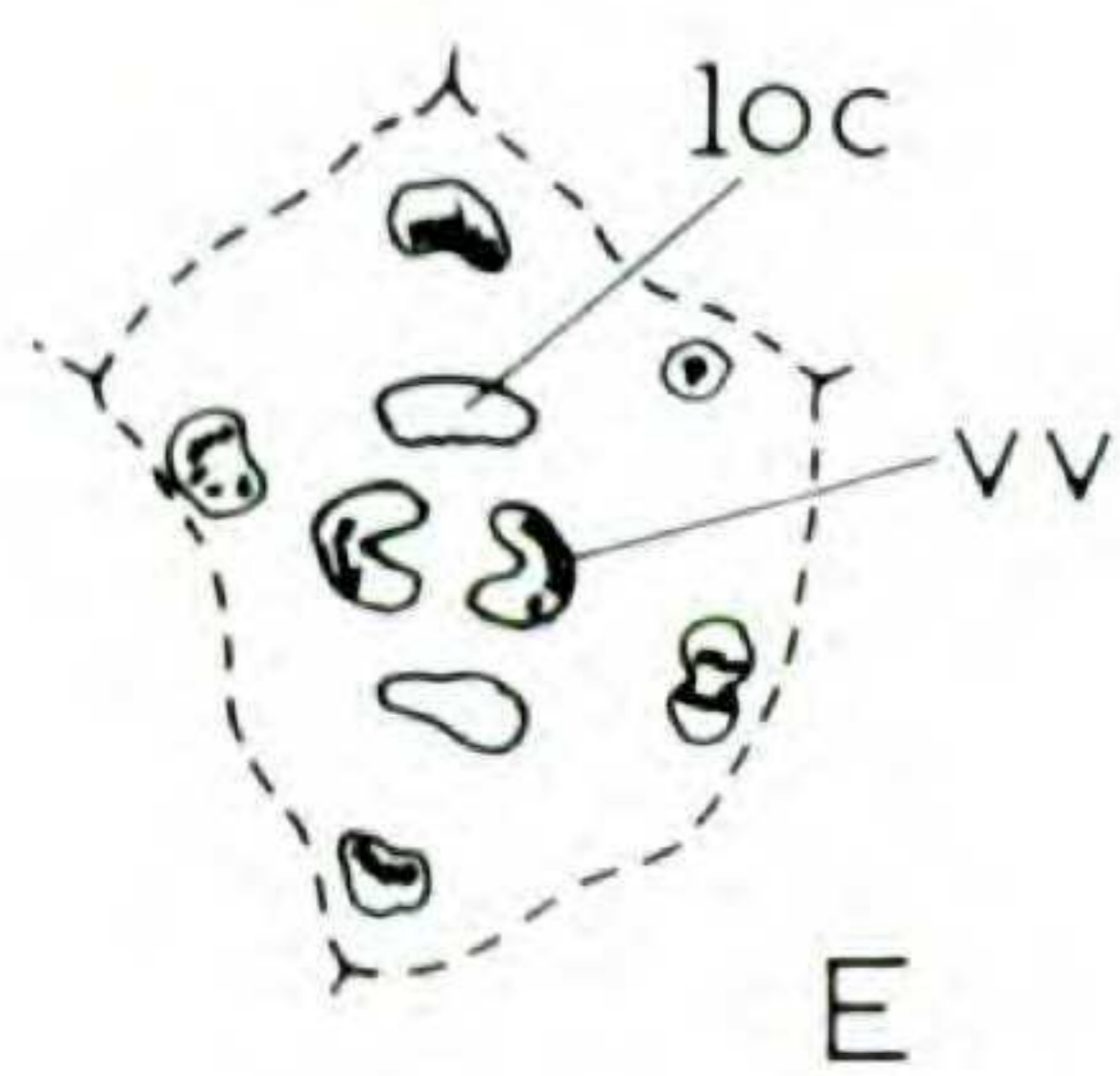
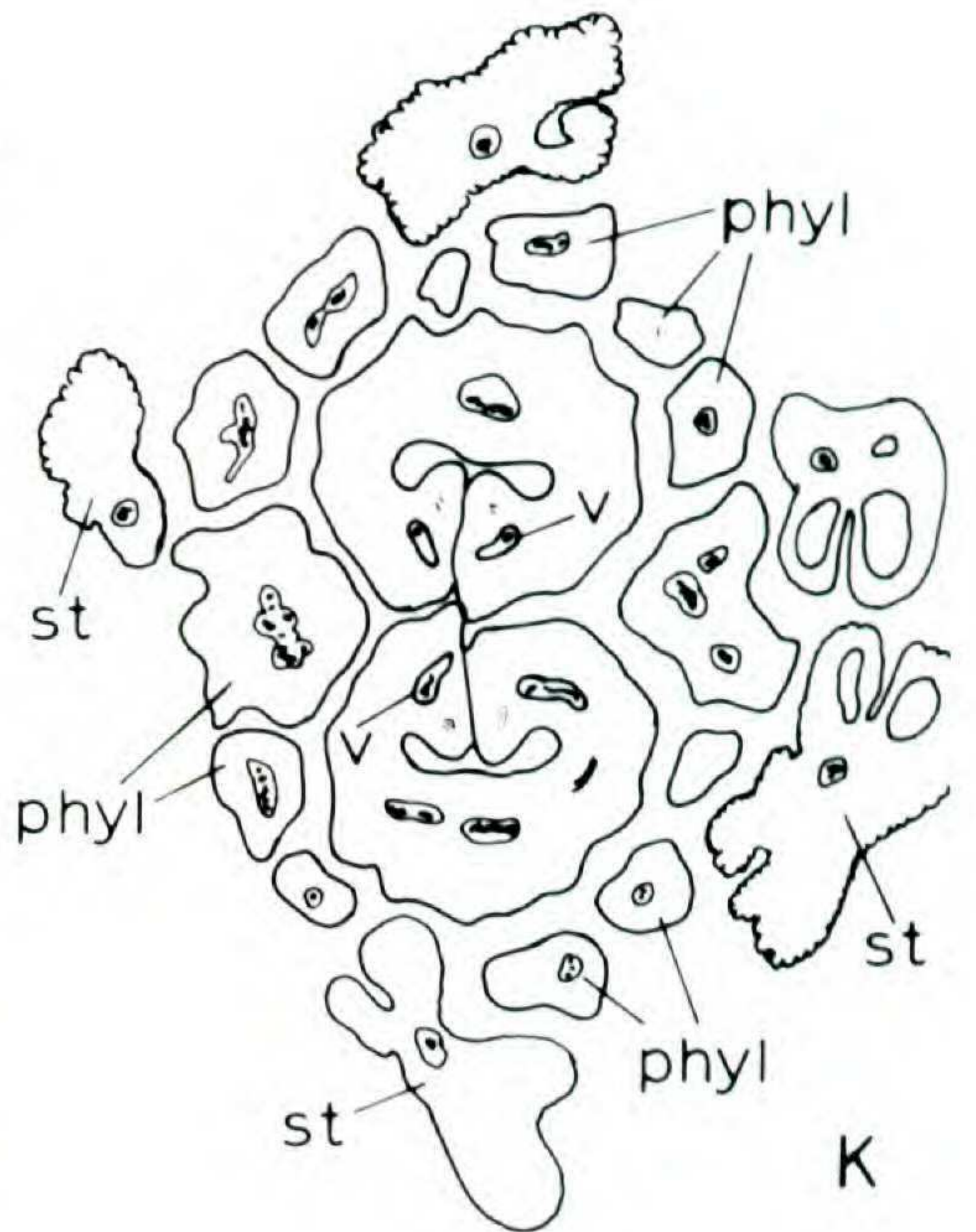
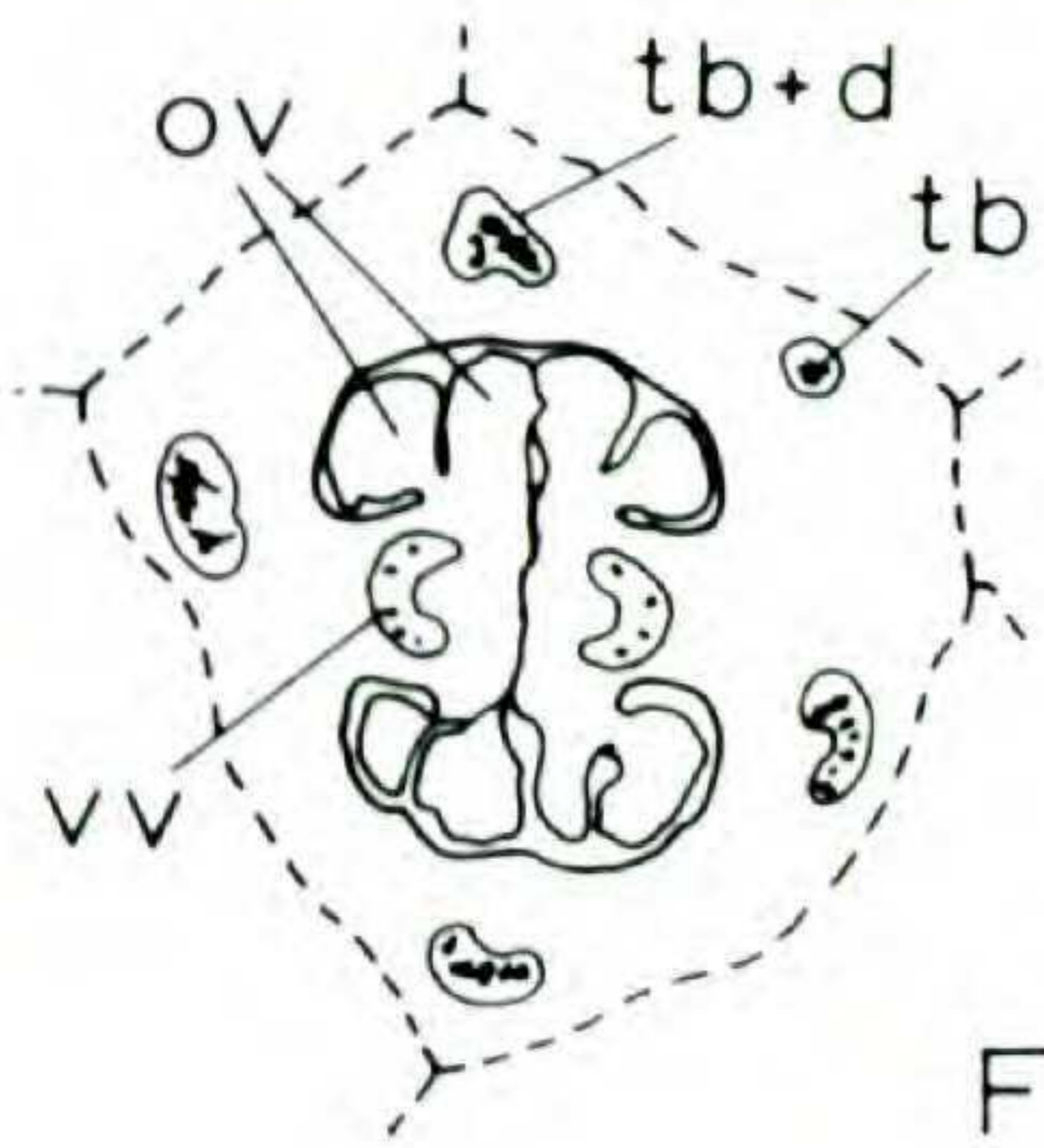
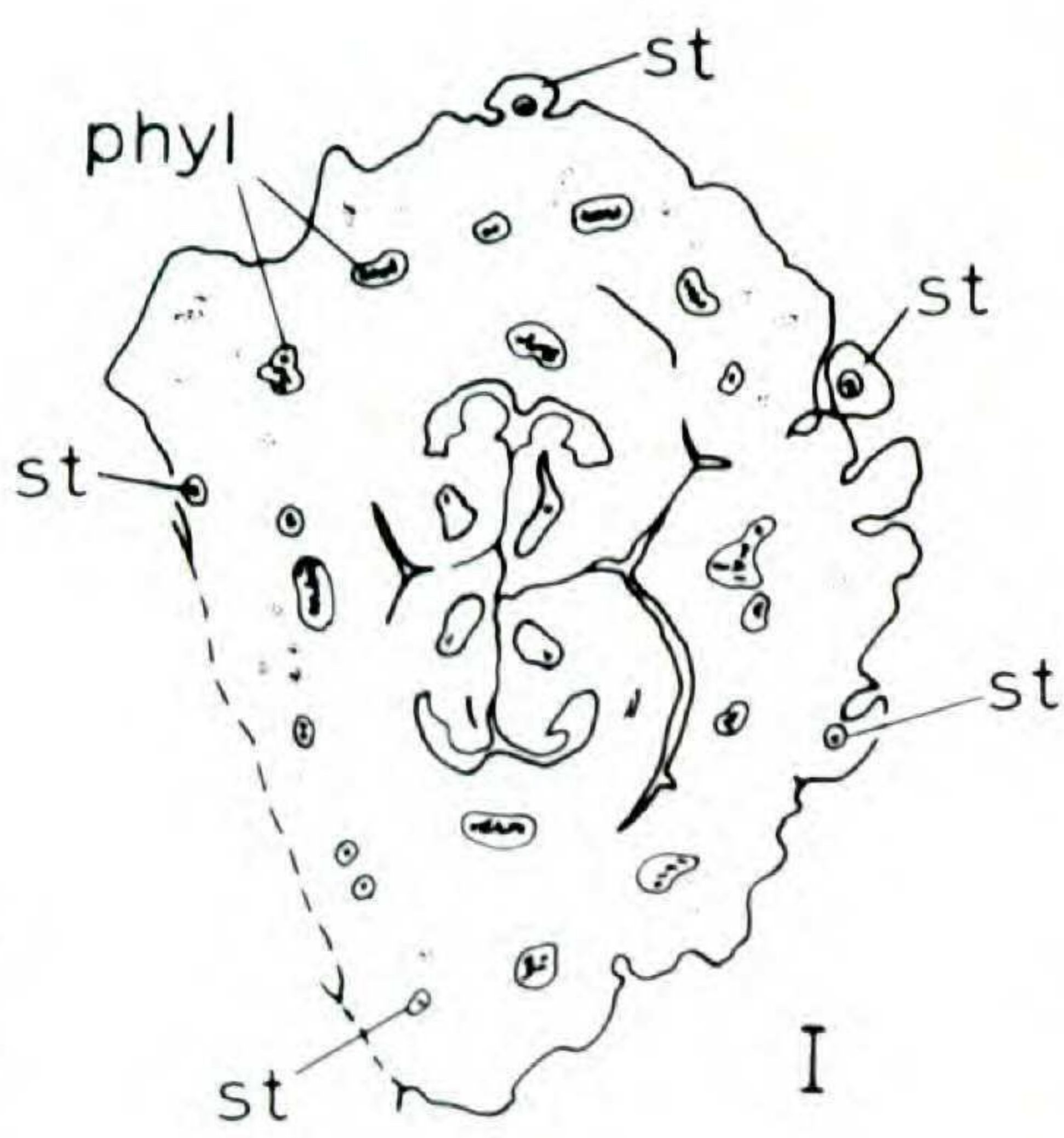
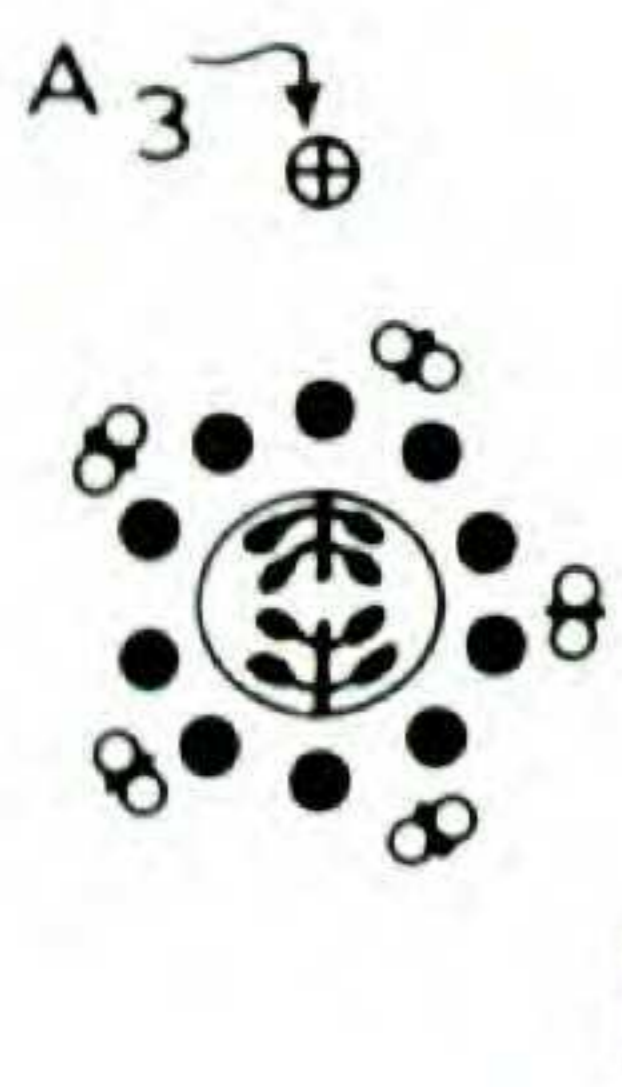
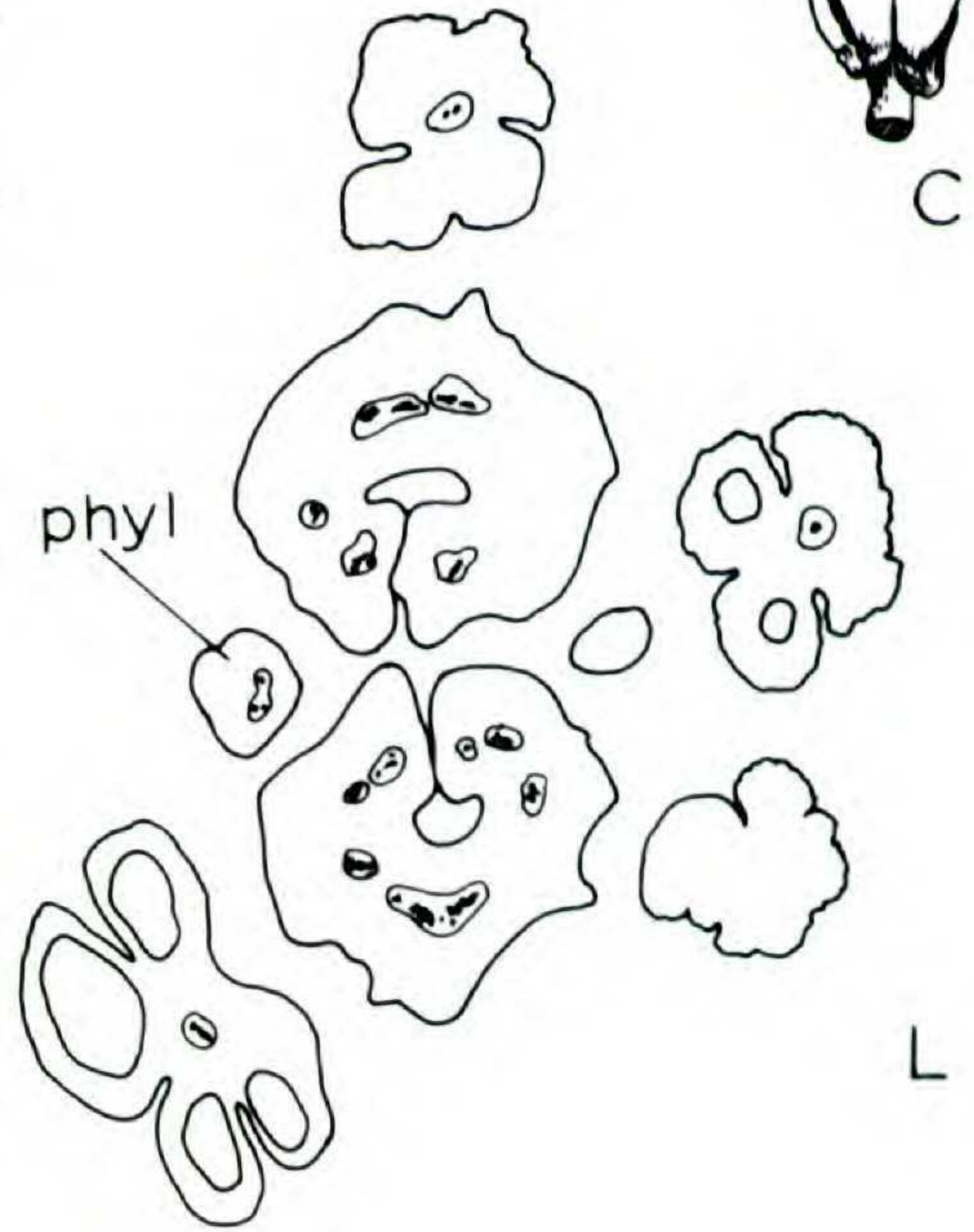
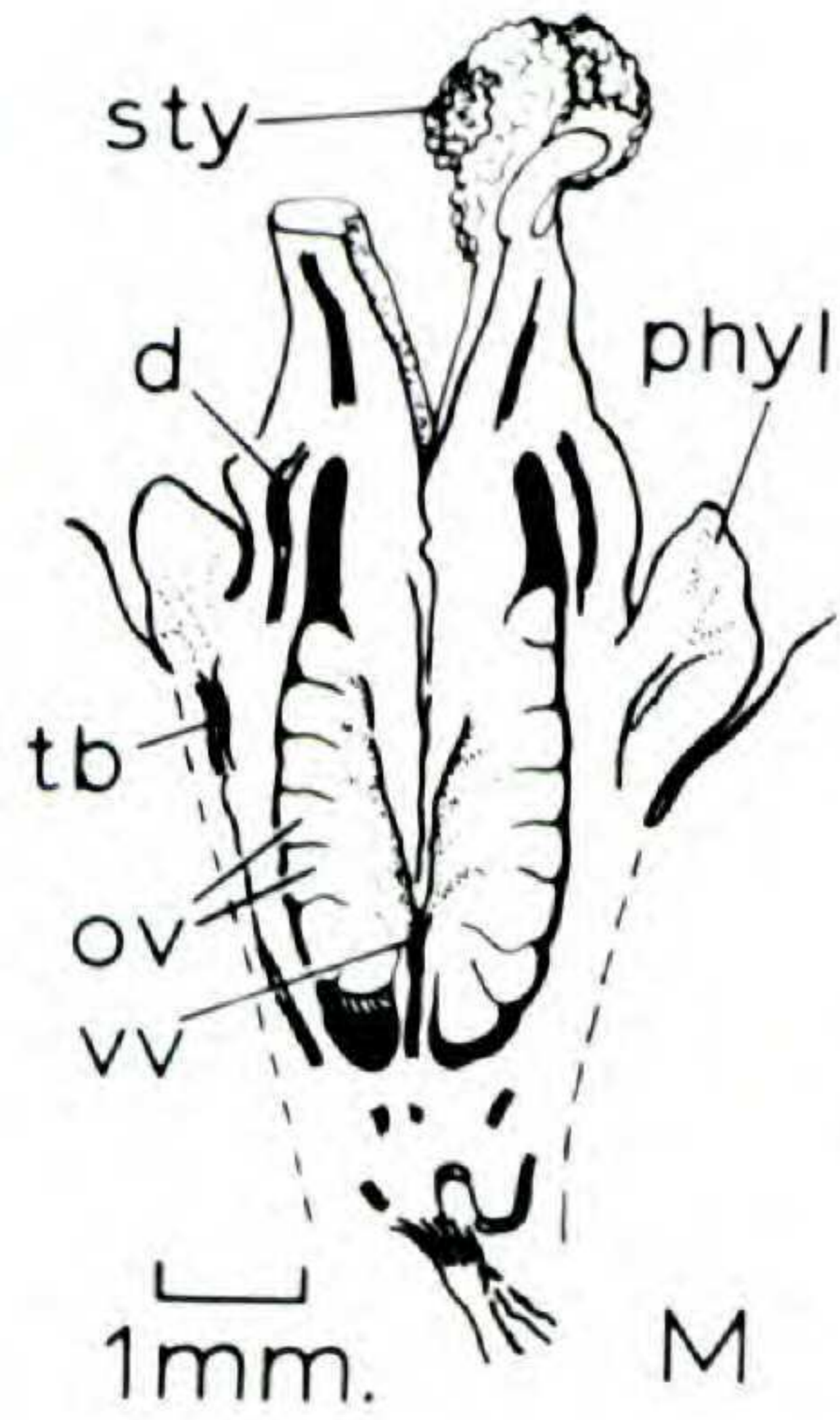
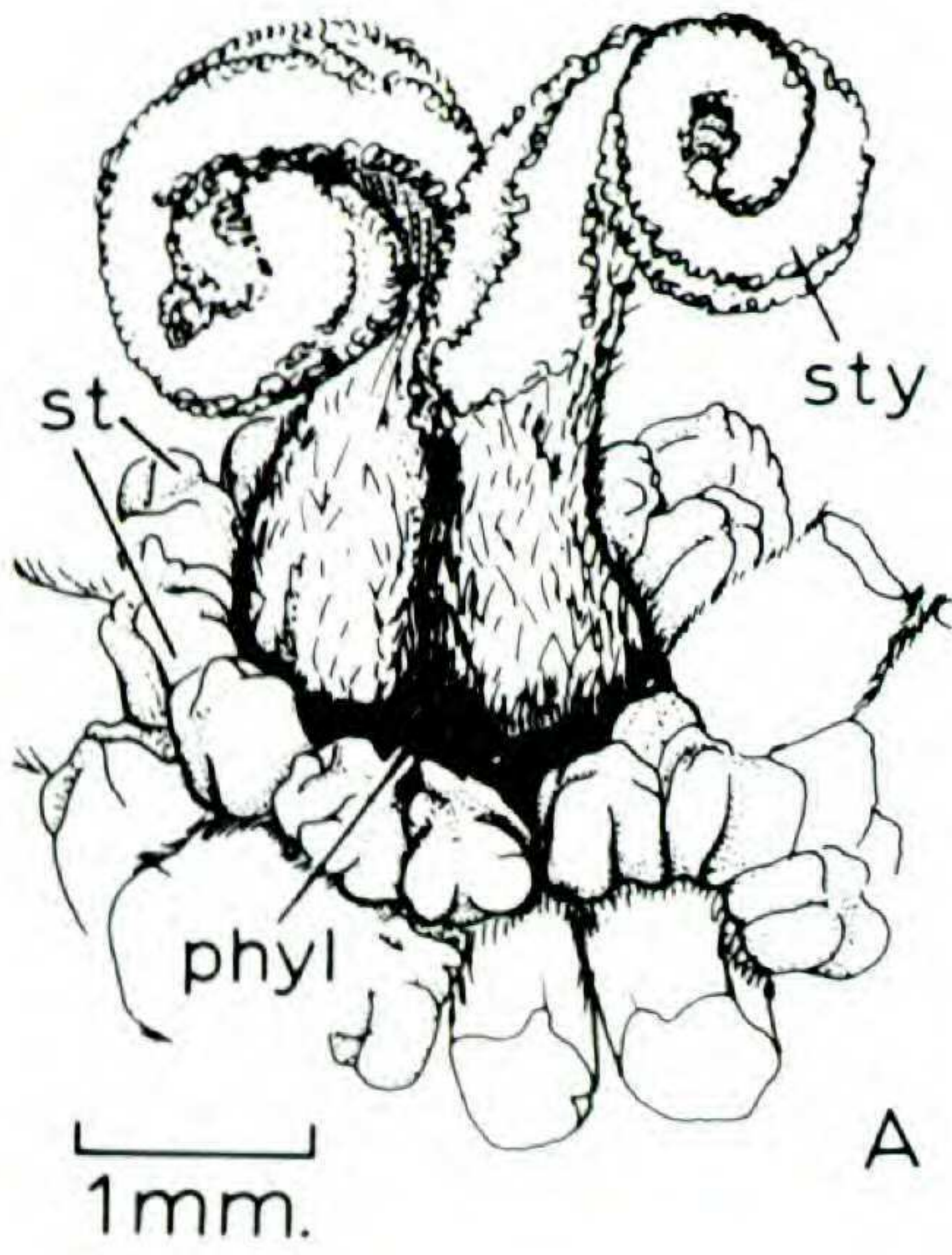
Pistillate flower. As in *Liquidambar*, I found no morphological evidence of a calyx or corolla (Fig. 5A, B). On the surface of the pistillate head three to ten stamens define the periphery of each flower. Their anthers are often rudimentary and misshapen, but in some cases they are fully formed and contain abundant pollen. The anthers are broadest abaxially, and the connective is frequently minutely apiculate adaxially (Fig. 5A). Stamens in which the anther connectives are elaborated into stylodia with stigmatic surfaces (Fig. 6F–H) have been observed in one specimen of *A. chinensis* (*Pételot 5944*, A). A cycle of short, inconspicuous, pubescent phyllomes occurs between the stamens and style bases (Fig. 5M). In maturing flowers the phyllomes appear broader and more massive, with more complex lobing than those in *Liquidambar*. The apocarpous portions of the two carpels are short, thick, and pubescent. Within the half-inferior ovary a shallow partial septum divides the base of the locule, but shortly gives way to two appressed parietal placentae (Fig. 5E, F). A count of the number of ovules per carpel margin in specimens at hand showed 12–16 (28–31 per carpel) in *Altingia chinensis* (*Pételot 5944*, A) to 20–25 (41–47 per carpel) in *A. excelsa* (*Bogle 583*). The ovules are anatropous and become angular to weakly winged at maturity.

The form of the sterile phyllomes varies among the species of *Altingia*. In most species these organs are short, broad, blunt, and pubescent structures (Fig. 5A, M). In a specimen of “*A. chinense*” from Tonkin (*Pételot 5944*, A), however, I observed subulate phyllomes (Fig. 6E) comparable to those of *Liquidambar formosana*, and similar subulate organs 4–6 mm long are described by H. T. Chang (1962, as “calyx limb”) in *Semiliquidambar cathayensis* H. T. Chang (*A. chingii* Metc. pro parte).

Staminate flower. The staminate flowers of both *Altingia chinensis* and *A. excelsa* are also similar to those of *Liquidambar*. The pedunculate secondary axis of a staminate head of *A. chinensis*, from which all the anthers have been removed, is illustrated in Figure 4G. The individual flowers are indistinct, having merged with the axis. In undistorted flowers a single cycle of stamens is inserted around the periphery of a shallow depression in the surface of the axis. The anthers are tetrasporangiate, with a broad, fleshy cap formed by the connective (Fig. 5C). The surface of the depression is very finely and minutely pubescent, catching many pollen grains. At either end of the depression the tip of an abortive carpel primordium is often evident. Each tip bears a tuft of hairs (Fig. 4G, arrows). The scars of three secondary bracts (B_2) are also apparent on the surface of this axis. Each secondary bract subtends a group of staminate flowers, the lowest of which are greatly distorted. The axis of this head thus represents at least three axillary floral clusters fused into a common mass. This morphological evidence suggests that the partial inflorescences of *Altingia* represent condensed branch systems comparable to those described for *Liquidambar styraciflua* by Wisniewski and Bogle (1982). However, similar studies in *Altingia* are needed.

Floral vascular anatomy. The principal basis for comparison with *Liquidambar* used here is the vascular anatomy of the functionally pistillate flowers. The vasculature of the staminate flowers is greatly reduced, modified and irregular, as in *Liquidambar*, and no attempt is made to describe it here.

Pistillate flower. Reduction of the peduncular and pedicellar axes in the pistillate heads in *Altingia* appears more advanced than that in *Liquidambar*, resulting in increased congestion of the flowers. The peduncular stele is expanded into a loose network of branching and anastomosing bundles, and the abbreviated, loosely



formed pedicellar cylinders seen in the receptacles of pistillate flowers of *Liquidambar* are absent here. An indication of the increased reduction and fusion within the heads is the occurrence of basal fusions between the trunk bundles of adjacent flowers. These bundles separate to their appropriate flowers at a relatively low level. Such fusions were not noted in the species of *Liquidambar*.

Several (five to seven) vascular bundles diverge directly from a gap in the peduncular stele into the relatively broad base of the sessile flower (Fig. 5D). These bundles may function simply as hypanthial trunk bundles, supplying traces to the stamens and the sterile phyllomes (fleshy, sterile "disk" lobes of Vink, 1957), or they may divide to supply dorsal or ventral bundles to the gynoecium as well. The number of trunk bundles corresponds to the number of stamens in most cases (Fig. 5E, F). As the trunk bundles ascend in the hypanthium they begin to branch at a level slightly below the separation between the carpels and the phyllomes (Fig. 5G). Each trunk bundle usually produces a trace (st) to a rudimentary stamen, as well as lateral branches (lb) to one or both sides. The latter may function directly in supplying the base of a phyllome or may anastomose with a lateral branch from an adjacent trunk bundle to form such a supply. Each major lobe of the cycle of phyllomes is thus supplied with a vascular bundle. Within the lobe the bundle ramifies to form a complex system of minor bundles, procambial at anthesis, many of which terminate in small protrusions on the abaxial side of each lobe (Fig. 5H–J).

At the level of separation of the carpels from the phyllomes the stamen and phyllome bases may appear fused for a short distance, as if in the rim of a hypanthial tube (Fig. 5I, J).

The formation of the carpel ventral bundles is

variable. They are formed immediately in the base of the flower, frequently before either dorsal bundle is evident. One to three vascular strands become associated at either side of the receptacle in the transverse plane to form a compound ventral bundle (vv in Figs. 5D, E, 6J). In some serial sections, and in some cleared flowers, the compound ventral bundles appear to consist of a central strand flanked on either side by minor lateral strands that diverge slightly, giving the impression of a second bundle in each carpel margin. In cleared material these divergent bundles are seen to persist for only about a third of the length of the ovary. In serial sections they are seen to dissipate in procambial strands to the lowest inserted ovules. They appear to represent minor placental strands of the ventral bundles, rather than a second bundle in each margin. A similar situation is seen in *Liquidambar styraciflua* (Fig. 6A, B).

At the level of insertion of the lowest ovules the compound ventral bundles (vv) divide, forming individual ventral bundles (v) to each of the adjacent fused carpel margins (Fig. 5G). Above this level the traces to the ovules originate from the free ventral bundles (Fig. 5H), which finally pass unbranched into the styles (Figs. 5J, 6J).

The carpel dorsal bundles (d) may be distinct at the base of the locules, but more often they are fused basally with one or more of the peripheral trunk bundles and do not separate until about halfway up through the inferior portion of the ovary (Fig. 5G).

Secondary carpel wall bundles appear only as the hypanthium begins to separate from the ovary. Above this level (Fig. 5I–L), lateral branch bundles pass directly from dorsal to ventral bundles, often almost horizontally. Each lateral is accompanied by a gum duct, as are the dorsal and ventral bundles. There is no evidence in my material

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 FIGURE 5. *Altingia excelsa* Nor.—A. Pistillate flower at anthesis. Parts of adjacent flowers shown.—B. Floral diagram.—C. Stamen from a staminate flower. D–L. Serial sections of a pistillate flower at anthesis.—D. Receptacle; several peripheral trunk bundles and compound ventral bundles evident.—E. Bases of locules.—F. Slightly above the locule bases, showing separation of the parietal placentae.—G. About mid-height in inferior portion of ovary, showing dividing compound ventral bundles, branching trunk bundles, ovular traces departing from ventral bundles.—H. Through upper part of inferior portion of the ovary; stamen traces and ramifying bundles to the phyllomes shown.—I. Partial separation of the hypanthium from the carpels, and of the carpels from each other.—J. Insertion of the stamens and phyllomes.—K, L. Sections through the style bases, showing phyllomes and anthers of the sterile stamens.—M. Drawing made from a longitudinal hand section through a pistillate flower in the median plane, showing numerous ovules, insertion of phyllomes. (Key: A₁, primary axis; A₂, secondary axis; d, dorsal carpel bundle; lb, lateral branch; loc, locule; ov, ovule; phyl, phyllome; st, stamen, stamen trace; sty, style; tb, trunk bundle; v, ventral carpel bundle; vv, compound ventral bundle.)

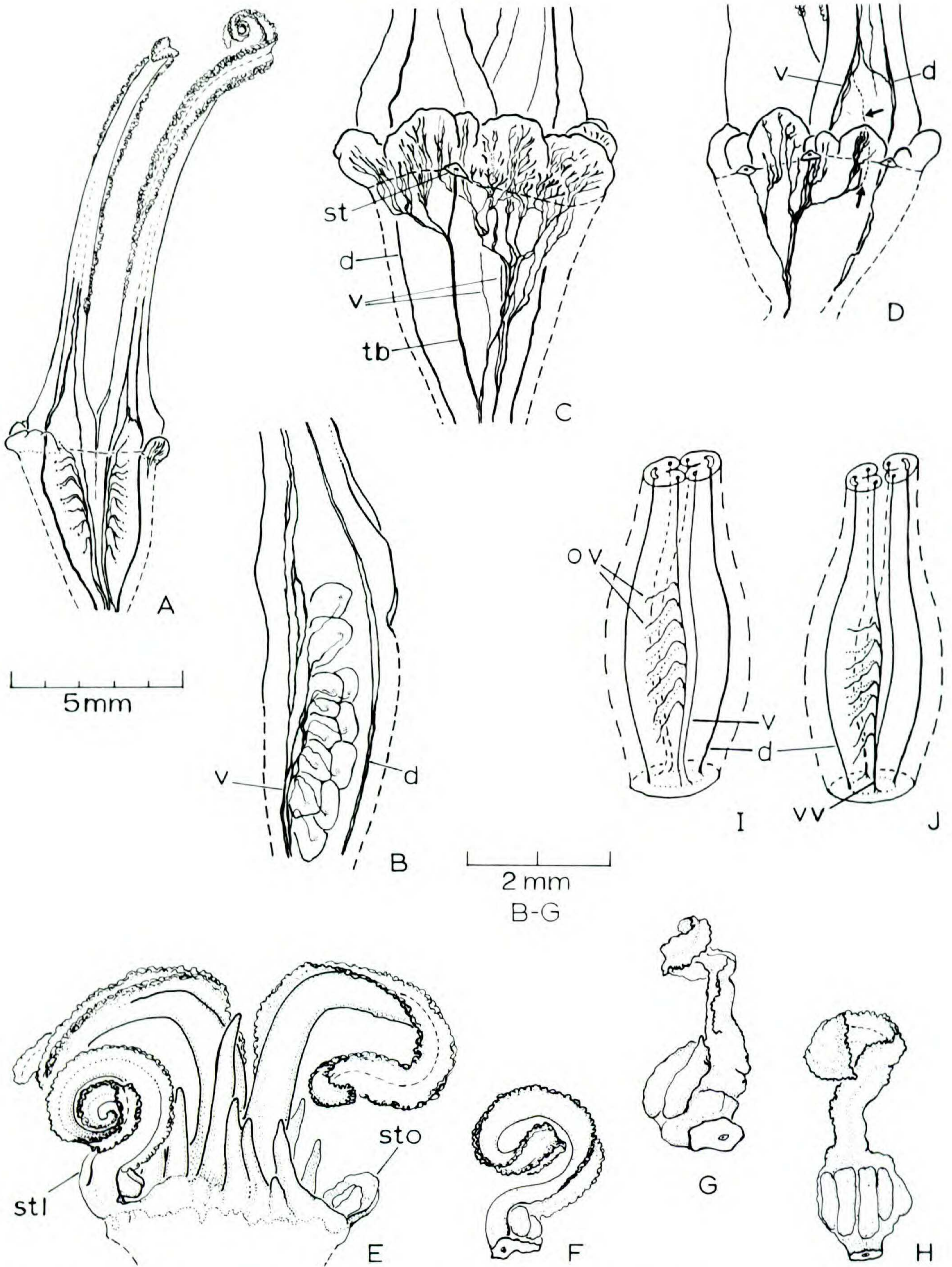


FIGURE 6. A-D. *Liquidambar styraciflua*.—A. Vasculature of gynoecium of the pistillate flower, showing dorsal and ventral carpel bundles, and the ovule traces originating from the ventral bundles on the near side (Bogle 823).—B. Vasculature of one carpel enlarged, showing dorsal bundle and ventral bundle of near margin with ovule traces; ovules outlined (Bogle 823).—C. Ramifying vascular supply to phyllomes of the pistillate flower; one stamen trace and insertion scar indicated. Note that one dendritic system supplies branches to more than one lobe of the cycle of phyllomes in both C and D (Bogle 823).—D. Less elaborate vascular supply to phyllomes of a pistillate flower (Bogle 790). E-H. *Altingia chinensis* (Pételot 5944).—E. Pistillate flower with one stylodeus stamen with half-anther (stl), one scale-like staminodeum with half-anther (sto) and numerous

of vascular bundles contributed to the carpel walls by the hypanthial bundles, as in *Liquidambar orientalis* and *L. styraciflua*.

DISCUSSION

The taxa of subfamily Liquidambaroideae exhibit an interesting combination of relatively primitive and advanced morphological and anatomical characteristics. The complex inflorescences are terminal on long or short vegetative axes. Subsequent vegetative growth develops from axillary buds.

Morphological evidence from mature inflorescences indicates that the total inflorescence in the subfamily is derived from a compound raceme by reduction, and that a minimum of three orders of axes (or four if the floral pedicels are taken into account) are present. Ontogenetic study of the total inflorescence of *Liquidambar styraciflua* (Wisniewski & Bogle, 1982) supports this interpretation.

The primary or central axis of the total inflorescence elongates at anthesis, carrying the partial inflorescences ("heads") out of the bud and separating them through internodal elongation. The internodes may become progressively shorter toward the tip of the axis, and the most distal internodes may fail to elongate, resulting in the aggregation of a few distal heads into an irregular common mass. One or two functionally pistillate heads usually occupy the lowermost node(s) of the central axis, whereas the remaining nodes bear functionally staminate heads. However, completely pistillate or staminate total inflorescences are not uncommon.

The secondary axes, often referred to as the peduncles of the heads, originate in the axils of primary bracts of the primary axis, and show varying degrees of reduction. The proximal ones may elongate considerably, producing long- to short-stalked heads bearing secondary bracts with axillary flower clusters, whereas the more distal ones may fail to elongate at all, resulting in heads sessile on the primary axis. Failure of the distal internodes of the secondary axes to elongate re-

sults in terminal compound clusters of flowers similar to those at the tip of the primary axis.

The tertiary axes that bear the several flowers of each cluster are generally abortive, as are the floral pedicels (quaternary axes), resulting in the aggregation and fusion of the flowers.

An abscission layer forms in the primary axis just above the node bearing the uppermost pistillate head, allowing the entire staminate portion of the total inflorescence to fall after anthesis and pollination. The pistillate heads enlarge greatly in fruit and fall only after the seeds are shed in autumn. Artificial pollinations have shown the three principal species of *Liquidambar* to be interfertile (Santamour, 1972), but I know of no similar experiments in *Altingia*, or between *Altingia* and *Liquidambar*.

The individual flowers of *Liquidambar* and *Altingia* are morphologically bisexual, but typically are functionally unisexual. Stamens occur in the functionally pistillate flowers and range from typically abortive staminodia to rarely fertile. When fertile the viable pollen may be shed well after stigma receptivity in the same flower, preventing self pollination (Schmitt, 1965). Abortive carpel primordia or rudimentary ovaries occur in some staminate flowers, but ovules have not been observed. The inflorescences and flowers clearly are adapted to anemophily and outcrossing.

There are numerous conflicting observations in the literature regarding the presence or absence of a perianth in the Liquidambaroideae. Although there is general agreement that the staminate flowers of both genera lack a perianth, there are several reports of a perianth in the pistillate flowers of both *Liquidambar* and *Altingia*. I believe that these reports are based on misinterpretation of either: 1) the cycle of sterile stamens (as suggested by Horne, 1914); 2) the cycle of elongate sterile phyllomes (disc lobes) that occurs between the stamens and carpels in *Liquidambar formosana* and some species of *Altingia* (as *Semiliquidambar*); or 3) a layer of sclerenchymatous tissue that forms between and unites

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subulate phyllomes (pubescence of phyllomes and styles omitted. —F–H. Three variants of stamens with stylodeus connectives, bearing two or four sporangia. I–J. Diagrammatic representations of carpel vasculature in Liquidambaroideae. —I. Adjacent ventral bundles (v) free of any fusion. —J. Adjacent ventral bundles fused for a short distance basally (vv). Ovule traces shown for only one ventral bundle. (Key: d, dorsal carpel bundle; ov, ovule, ovule trace; st, stamen, stamen trace; stl, stylodeus stamen; sto, staminodium; tb, trunk bundle; v, ventral carpel bundle; vv, compound ventral bundle.)

the inferior portions of the flowers in the pistillate heads, and becomes protrusive as the heads dry out at maturity.

In *Liquidambar* various workers have described what they considered to be perianth parts (Oliver, 1867; Sargent, 1890, 1922; Ek, 1902; Sosa, 1978). Oliver (1867) apparently considered the sterile phyllomes of all three species of *Liquidambar* to be calycine. The indurated peripheral rim between flowers of mature heads of *L. styraciflua*, considered by Sargent (1890, 1922) to be a rudimentary calyx, is more probably formed by layers of bony tissue (possibly the "epidermal hairs" or "hair-like cells" of Schmitt, 1965) that externally delimit and unite the hypanthial walls of the fused, half-inferior ovaries that form the female partial inflorescences. The distal margins of these bony layers become protrusive in the surface of the head as the parenchymatous tissues of the fruits dry out and collapse.

Endress (1977) stated that "a perianth is almost totally lacking" in subfamily Liquidambaroideae, while Niedenzu (1891), Harms (1930), Samorodova-Bianki (1957), and Schmitt (1965) all found the pistillate flowers to lack a perianth in *Liquidambar*.

In *Altingia*, references to a perianth in the pistillate flowers are common. Blume (1828) apparently interpreted the sterile stamens as calyx lobes. Several workers described calyces united between flowers, but lacking a limb (e.g., Guillaumin, 1920; Hutchinson, 1967), or immersed in a disc with connate calyces fused with the stamens (Nakai, 1943). Several authors appear to have interpreted the sterile phyllomes (disc lobes) as part of the calyx limb (Griffith, 1836; Hooker & Thomson, 1858; Clarke, 1858; Niedenzu, 1891; Noronha, 1790), whereas the remainder believed that a perianth is almost totally lacking (Endress, 1977), or absent (Hemsley, 1906; Schulze-Menz, 1964; Tong, 1930; Wilson, 1905; Vink, 1957).

In *Semiliquidambar* H. T. Chang, Chang (1962) described the pistillate flowers as having confluent calyces with subulate calyx limbs ranging from 1–6 mm long. In a comparative chart he listed the calyx lobes as persistent or obscure in *Liquidambar*, persistent in *Semiliquidambar*, and lacking in *Altingia*. However, in fruits of *Altingia chingii* Metc. [= *Semiliquidambar chingii* (Metc.) Chang] that I have seen (*Lau* 4356, *Tso* 20760, both A) the only structures of the dimensions described are sterile phyllomes.

In the many specimens of *Liquidambar* and *Altingia* that I have examined I have found no evidence of calyx lobes or limb in any of the staminate or pistillate flowers at anthesis or beyond and have to conclude that none exist. Nor is there any evidence of a perianth in the earliest ontogenetic stages of *Liquidambar styraciflua* (Wisniewski & Bogle, 1982). However, I assume, as have others (Guillaumin, 1920; Hutchinson, 1967), that a calyx or calycine tissue was present in the ancestral line, forming a hypanthium that is now incorporated into the head as confluent tissue between the pistillate flowers. It may be this tissue that forms the interlocking "hair-like cells uniting the adjacent capsules" described by Schmitt (1965, fig. 2), and which eventually produces the sclerotic tissue uniting the ovaries of the flowers. I base my assumption that a perianth limb has been lost, rather than that the flowers were primitively naked, on comparative evidence from closely related subfamilies that also have their flowers fused in heads or spikes to some degree. In the dichlamydeous flowers of *Rhodoleia* (Rhodoleioideae) a very reduced, membranous, inconspicuous calyx is present. In the Exbucklandioideae (including Mytilarioideae H. T. Chang, 1973), *Mytilaria* is dichlamydeous with distinct calyx lobes, *Exbucklandia* is also dichlamydeous but shows evidence of a calyx only in the early stages of floral ontogeny, and *Chunia* lacks both calyx and corolla. *Disanthus* (Disanthoideae) is dichlamydeous, with distinct sepals and petals. It appears that reduction or loss of perianth in Liquidambaroideae, Rhodoleioideae, and Exbucklandioideae is related to condensation of inflorescences and increasing degrees of fusion between flowers in the heads. In this process, reduction and loss of the calyx limb may precede that of the corolla (Bogle, pers. observ.). Loss of the perianth has apparently occurred independently in both Liquidambaroideae and Exbucklandioideae, as well as in the more advanced members of the subfamily Hamamelidoideae (Bogle, 1970; Endress, 1970, 1978).

As is apparent from the foregoing discussion of the perianth, the interpretation of the cycle of sterile phyllomes (disc lobes) has been problematical. I have used the term phyllome (sensu Esau, 1965: 424, 540) to distinguish these organs from sterile and reduced stamens (staminodes), which commonly occur in pistillate flowers, because they show no direct relationship in structure or in transitional forms to stamens. Just as some authors considered them calycine, others have in-

terpreted them as bracteoles surrounding the pistillate flowers (Guillaumin, 1920); as vestigial styles of sterile flowers interspersed among the fertile flowers (Harms, 1930); as staminodia (Tong, 1930); as "disk" lobes (Vink, 1957); as papillae on the surfaces of the capsules (Schmitt, 1965); or as the sterile setae ("borsten") of *Liquidambar formosana* on which Harms (1930) based his section *Cathayambar*. Similar elongate sterile bodies, comparable to those seen in *L. formosana*, also occur in some species of *Altingia*, where I believe they have been interpreted as calyx lobes (H. T. Chang, 1962, 1973, as *Semiliquidambar*).

Croizat (1947) considered the lobes or sterile phyllomes to be "scales" arising "from the body of the head, or torus," and that the staminodia surrounding each flower "either belong to the scales that immediately surround the carpels, or to a row of subsidiary undeveloped scales abaxially located from these." He wrote that *Liquidambar* is "in active evolution away from the amentiferous stage, still retaining the head- or ament-like inflorescences and an ambiguous sexual expression, which leads on occasions to purely male or female heads or flowers."

However, the vascular supply to the phyllomes arises from the same trunk bundles as that of the stamens and carpels, and at a relatively high level within the flower. This does not support an interpretation of the phyllomes as extra-floral scales arising de novo from the torus. Neither does it support an interpretation of them as extra-floral organs of any kind.

Vink (1957: 364) emphasized the position of the sterile phyllomes (as "disk lobes") in *Altingia* and *Exbucklandia* (as *Symingtonia*) between the stamens and ovary. This position might suggest that they are staminodia, glandular tissue, or reduced sterile carpels.

Tong (1930: 9, 13, 14, fig. 2C, D) interpreted the phyllomes as staminodia, noted their spine-like ("stachelformig") form in *Liquidambar formosana*, and cited staminodia with functionless anthers as transition forms from stamens to staminodia in pistillate flowers of both *Liquidambar* and *Altingia*. His diagram (1930, fig. 2D) of the staminate flower of *Liquidambar* indicated two cycles of stamens. I have not observed this condition, nor have I seen any evidence of sterile phyllomes with abortive anthers. I have seen stamens with stylodeus elaborations of their connectives (Fig. 6E–H) external to the cycle of phyl-

lomes, but the adjacent phyllomes show no such modification. The resolution of the proliferated vascular supply in the base of the phyllomes to a single, central vascular bundle in their distal portions could suggest the single bundle that normally supplies each stamen.

The short, blunt, glabrous phyllomes in *Liquidambar styraciflua* and some *Altingia* species look somewhat like similar organs in *Rhodoleia* and *Exbucklandia*, however. In *Rhodoleia* these organs form a cycle of very small, glabrous, irregular lobes inserted between the stamens and the ovary and are reported to be glandular (Leeuwen, 1938). In *Exbucklandia*, however, a cycle of blunt, glabrous, fleshy lobes is elevated on the inner rim of the hypanthium, and is clearly separated and distinct from the gynoecium. These lobes are not reported to function as glands, and their position on the rim of the hypanthium suggests a relationship to the androecium.

The proliferated system of procambial strands seen in the base of the sterile phyllomes or the stomata in the phyllome epidermis of *L. styraciflua* (Wisniewski & Bogle, 1982) might also suggest a glandular or secretory function, but there are no reports in the literature, nor any field observations of mine, that indicate such activity in these organs. Nor do the pubescent surfaces of the phyllomes of *Liquidambar formosana* and *Altingia chinensis* suggest a glandular function. In these species the epidermal trichomes of the phyllomes and the styles are similar and are not glandular.

A gynoecial origin could be inferred from the styliform phyllomes of *Liquidambar formosana*, and to a lesser extent from some specimens of *Altingia* (as *Semiliquidambar*) in which these organs approach the functional styles in length, and bear the same type of pubescence. Although they look very much like abortive carpels both at anthesis and in fruit, and have been interpreted as such (Harms, 1930), I have seen no evidence of stigmatic surfaces or ovule production in any of them. Many specimens of other species of *Liquidambar* and *Altingia* have relatively short, blunt, glabrous phyllomes, which sometimes appear to be inserted on the vestige of a hypanthial tube, apart from the ovary.

The late appearance of the phyllomes in ontogeny (Wisniewski & Bogle, 1982), after the stamens and functional carpels are initiated (at least in *Liquidambar styraciflua*) neither establishes nor eliminates a gynoecial relationship, but the ramifying vascular supply to the base of the phyl-

lomes does not appear comparable to that of the functional carpels.

A secondary origin of the sterile bodies might be hypothesized if some function relating to pollination or the reproductive process could be confirmed for them, as in *Rhodoleia*. On the other hand, the presence of similar whorls of sterile organs in such divergent genera as *Liquidambar*, *Altingia*, *Rhodoleia*, and *Exbucklandia* suggests an origin in a common ancestry, rather than a secondary origin related to reproductive processes.

It seems probable that the interpretation of the sterile phyllomes in Liquidambaroideae may relate directly to that of the similar organs in Rhodoleioideae, Exbucklandioideae, and Hamamelidoideae. If such fleshy, indeterminate organs were brought into close association with the developing gynoecium as a result of the condensation of the inflorescence, crowding of flowers, and eventual nearly complete fusion of hypanthium and gynoecium, morphogenetic factors might influence their development toward a stylodial morphology. That is not to suggest that Exbucklandioideae or Rhodoleioideae are in any way ancestral to the Liquidambaroideae, but rather that these groups probably shared a relatively close, common ancestral stock. The flowers of *Mytilaria* (Exbucklandioideae), with a dicyclic androecium in which the inner cycle of stamens appears to be sterile, and in which all stamens have remarkable fleshy, horned extensions of the anther connective, may provide clues as to the origin of the sterile phyllomes of the Liquidambaroideae. Additional ontogenetic studies in Liquidambaroideae, Rhodoleioideae, and Exbucklandioideae are needed.

The gynoecium in the Liquidambaroideae is the most primitive in the family. The carpels are follicular and unsealed. The shallow partial septum in the base of the unilocular ovary is characteristic of the family and becomes progressively more prominent in more advanced members of the family. The extensive stigmatic surfaces are clearly adapted for wind pollination. However, anemophily is probably a derived condition that has evolved several times within the family.

The carpel vascular supply of two marginal ventral bundles and a median dorsal bundle is comparable to that in the Rhodoleioideae, Exbucklandioideae, and Disanthoideae, and differs from the five bundle carpels of the Hamamelidoideae (Bogle, 1967, 1970). The ventral bundles

of adjacent fused carpel margins may be distinct or fused basally for a short distance. The latter condition is shared with Rhodoleioideae and also becomes more pronounced in other subfamilies.

The large number of ovules per carpel, and their insertion in more than one row on both margins, is in keeping with the primitive condition of the carpels. Only the basal or sub-basal ovules on each margin are fertile, the remaining ovules are presumably sterile by reduction. The number of seeds produced per flower is very low in relation to the total number of ovules initiated in each flower. The tendency toward ovule abortion and reduction in number that characterizes the family, culminating in one ovule per carpel in some genera of Hamamelidoideae (Bogle, 1970), appears to be well established in the Liquidambaroideae.

Placentation has been described as either axile or parietal in the Hamamelidaceae. In the Liquidambaroideae the lowermost ovules may be inserted on the partial septum in the base of the ovary. This condition is sometimes termed axile placentation. Most of the ovules are inserted above the partial septum on the two lateral compound placentae, hence placentation is parietal. At a still higher level the uppermost ovules may be inserted on free carpel margins. Consequently, I use the term parietal as defined by Lawrence (1951: 763): "borne on the walls within a simple or compound ovary, or on intrusions of the wall that form incomplete partitions or false septa within the ovary."

There has been some disagreement concerning the taxonomic relationships of *Altingia* (Noronha, 1790) and *Liquidambar* (Linnaeus, 1753). They were considered to be congeneric under *Liquidambar* by several early workers (Blume, 1828; de Candolle, 1830; Lindley, 1836, 1853; Oken, 1841; Bentham, 1861), and more recently by Leroy (1982). Bentham and Hooker (1865) and other subsequent workers have recognized them as distinct genera.

The major differences between the two genera are the more or less elliptic to oblong, pinnately-veined, persistent leaves of *Altingia*, as opposed to the palmately-lobed and -veined, deciduous leaves of *Liquidambar*. The segregate genus *Semiliquidambar* H. T. Chang is described as being intermediate between *Altingia* and *Liquidambar* in this respect, with leaves polymorphous (trilobate, simple, or lobed on one side), triplinerved, and deciduous or not (H. T. Chang, 1962). *Semiliquidambar* occupies an extensive area of

overlap between *Altingia* and *Liquidambar formosana* in southeastern China and on the island of Hainan (distribution map in H. T. Chang, 1962). This distribution suggests that some of the specimens attributed to *Semiliquidambar* may have originated as hybrids between *Altingia* and *Liquidambar*. The appearance of the subulate phyllomes seen in the pistillate flowers of these specimens may thus be inherited from a *L. formosana* parent. Further morphological investigations of *Semiliquidambar*, and attempts at controlled hybridizations between *Altingia* and *Liquidambar* such as those conducted in *Liquidambar* by Santamour (1972), would be highly desirable.

A curious parallel can be seen between the Hamamelidaceae and Platanaceae in that similar contrasting leaf forms occur in *Platanus*. The tropical, southeast Asian *Platanus kerrii* has persistent, elliptic to oblong, penninerved leaves, whereas the remaining species of the genus have deciduous, palmately-lobed and -veined leaves. On the basis of these and other morphological characteristics, Leroy (1982) recently proposed the establishment of two subgenera in *Platanus* to separate these two divergent forms. Should the intermediate form attributed to *Semiliquidambar* eventually prove to originate in hybridization between *Altingia* and *Liquidambar*, these two genera might warrant similar taxonomic treatment.

CONCLUSIONS

It now seems clear that the total inflorescence in the Liquidambaroideae is more complex than was formerly thought. Four orders of axes (including the floral pedicels) are present, but only those of the first and second order are obvious. Primary and secondary inflorescence bracts are present, but tertiary bracts subtending individual flowers have not been observed.

The flowers are potentially bisexual, becoming functionally pistillate or staminate through failure of the stamens or carpels, respectively, to develop. Unisexuality is not completely established.

There is no morphological or anatomical evidence of a perianth in early ontogeny or in mature flowers. The perianth limb is assumed to have been lost phylogenetically as a function of inflorescence condensation leading to crowding and fusion of flowers. However, there is the suggestion of a brief hypanthial tube in the fused bases of the stamens and phyllomes.

The stamens are few and variable in number in each flower, dehiscent laterally by means of longitudinal slits. The connective often forms a fleshy cap above the sporangia in staminate flowers. Each stamen receives a single vascular trace.

The cycle of sterile phyllomes develops between the stamens and carpels of pistillate flowers. The phyllomes are not clearly staminodial or carpellary in form, origin, or vascularization and are not known to have glandular or secretory function or a role in pollination. They may relate directly to similar cycles of sterile organs in Rhodoleioideae and Exbucklandioideae.

The partly inferior ovary is usually bicarpellate. The carpels are involute and follicular, with numerous ovules on each margin, but usually have only one fertile ovule at the base of each margin. The carpel margins are not sealed in their apocarpous portions. Each carpel receives a dorsal and two ventral bundles. The ovules are supplied from the ventral bundles.

Although seemingly specialized and advanced within the family in such characteristics as inflorescence structure, tendency toward unisexual flowers, distinctive pollen morphology, and anemophily, the Liquidambaroideae, nevertheless, have a more primitive gynoecium (with follicular carpels, three distinct vascular bundles in each carpel, and numerous ovules on each margin) than any other genus in the family. The gynoecium of the Rhodoleioideae most closely approaches that of Liquidambaroideae, and that of the Disanthoideae shows considerable modification from both of those groups. The gynoecial structure, in particular, of Liquidambaroideae represents the least specialized condition in a family in which the general trend is toward reduction in the gynoecium, decrease in the number of ovules to one per carpel, and increased connation of carpels and carpel bundles. When this is taken in conjunction with such specialized characteristics as the presence of resin ducts, condensed inflorescences, unisexual flowers, rugate to porate pollen associated with anemophily, and sterile floral organs (phyllomes) of uncertain nature, each characteristic occurring in at least two other subfamilies, the Liquidambaroideae can be seen as part of a continuum or reticulum within the Hamamelidaceae, rather than as an independent family, the Altingiaceae.

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